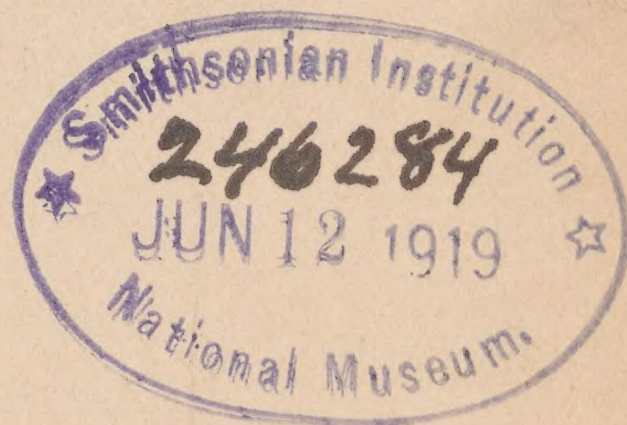
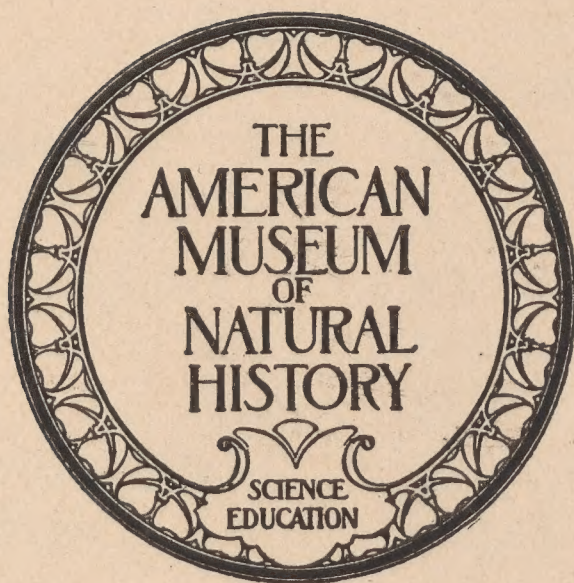


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ERRATA

Page 73, last line in foot-notes, for Vol. XXXIX read XXXIV.

“ 109, line 9 from bottom, for *depectus* read *despectus*.

“ 216, Fig. 16, for *Plianchenia* read *Pliauchenia*.

“ 318, line 21 from bottom, for synonym read synonymy.

“ 325, top line, for *L. caligenosus* read *L. caliginosus*.

“ 358, last line, for *Hyperooden* read *Hyperoodon*.

Plate XLIII, in B. and D., for (*Spenodon*) read (*Sphenodon*).

BULLETIN
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Article I.—NORTH AMERICAN CICADELLIDÆ IN THE COLLECTION OF THE AMERICAN MUSEUM OF NATURAL HISTORY. SUBFAMILY CICADELLINÆ

BY CHRIS E. OLSEN

Through the courtesy of The American Museum of Natural History, I have been accorded the privilege of studying the Cicadellidæ in the collection of this institution. Much of the material is from localities which are not readily accessible. The specimens are in good condition but a large part of them have yet to be determined and arranged. It may be said that this group, as well as the other homopterous insects in the Museum, has received but slight attention and urgently needs to be studied in order to do justice to those who have aided in building up the collection.

Among those who have previously worked on this material should be mentioned Dr. Herbert Osborn and Mr. E. P. Van Duzee. They have identified a large part of the already named material, most of which needed only arrangement and some slight changes in nomenclature. There were about 500 specimens; more than 400 were collected in what is embraced in Van Duzee's "S. E.," viz., Connecticut southward to Georgia and Florida; less than 100 are from thirteen other states outside of this. North Carolina and Florida are best represented in specimens, the latter yielding the best material; New York and New Jersey are next; Arizona is represented by 61 specimens. In Van Duzee's new list 12 genera, 48 species, and 9 varieties are given for this group. I have been able, so far, to find 10 genera, 29 species and 3 varieties in this collection. One new species is added to the list.

The collection is mostly eastern and southeastern, but there can still be added from these regions 7 species and 4 varieties. We have, thus, about 80% of the Eastern species.

The nomenclature used is that of Van Duzee's recent 'Check List of Hemiptera of America North of Mexico' (New York Ent. Soc., 1916). Many changes of nomenclature have been made in that work, particularly in the group with which this paper deals. This is not the place to go into details concerning the merits of Van Duzee's List; it must, however, be cited as a great contribution towards straightening out the nomenclature. He makes the genus *Tettigoniella* Jacoby (1903, = *Tetigonia* Kirkaldy, 1900) a synonym of *Cicadella* Latreille (1817) with *viridis* Linné (1758) as orthotype; then, the name Jassoidæ, Van Duzee (1892), is dropped as a synonym of Cicadellidæ, Latreille (1825); and, further, the group *Tetigoniini* Kirkaldy (1906, = *Tettigoniellini* Jacoby 1903) is thrown out entirely and a new name, Cicadellini (Subfamily, Cicadellinæ), is used. This does away with the misspelled name *Tetigonia* and all other names based on this; it is to be hoped that it will remain thus.

Oncometopia undata (Fabricius). Well represented from many localities in Pennsylvania, North Carolina, and Florida. One specimen from Florida was labeled *Proconia nigricans* Walk.; this is one of Walker's many synonyms, of which there are seven others attached to the above name.

Oncometopia lateralis (Fabricius). Valley of Black Mts., N. C., June 21–Aug. 17 (Beutenmüller). Clearwater and Sanford, Fla., April 26–29 (Van Duzee). Coyote Mts., Ariz., Aug. 4–7; near Kits Peak, Baboquivari Mts., Ariz., Aug. 7–9; near Bear Wallow, Santa Catalina Mts., Ariz., July 12–17 (Lutz). Estes Park, Colo., July 5, Alt. 7,500 ft. (Butler). Boulder, Colo., July 27. The specimens from North Carolina are typical; but those from Arizona and Colorado are smaller, their veins are less marked with black, and, as a whole, they appear to be a geographic race of the true species. However, further study and more material is needed to ascertain this.

Homalodisca triquetra (Fabricius). Sanford and Clearwater, Fla., April 28–29 (Van Duzee). Brownsville, Tex., April.

Aulacizes irroratus (Fabricius). Black Mts., N. C., May–Sept. (Beutenmüller). Crescent City, Fla., April 23 (Van Duzee). Orange Grove, Fla., May (Siefert). Deep Lake, Fla., April 13, labeled "*A. guttata* Uhl.?" (Grossbeck). One old abdomenless specimen from New York (Edwards Coll.). The species is rather rare in New York and northward.

Cicadella viridis (Linneus). Silkeborg, Denmark (Jensen Haarup). The writer has added this to the collection; it occurs in Canada and is the type species of the *Cicadellidæ*.

Cicadella hieroglyphica (Say). Phoenix, Arizona (Kunze Coll.).

Cicadella hieroglyphica var. **dolobrata** (Ball). Boulder, Colo., July 6.

Cicadella hieroglyphica var. **uhleri** (Ball). Phoenix, Arizona (Kunze Coll.).

Cicadella gothica (Signoret). Abundantly collected in New York and New Jersey. Other specimens from Gray Beard Mts., N. C., May 26; Black Mts., N. C., May-Aug.; Valley of Black Mts., N. C., July 5-Aug. 21 (Beutenmüller). Little Dear Is., Me., Sept. 10 (Zabriskie). Colorado Springs, Col., June 15-30, Alt. 6,000-7,000 ft. (Wickham in the Zabriskie Coll.).

Cicadella circellata ? (Baker). Coyote Mts., Ariz., Aug. 4-7; Sycamore Canyon, Santa Catalina Mts., Ariz., Aug. 20; near Kits Peak, Baboquivari Mts., Ariz., Aug. 7-9 (Lutz).

Cicadella occatoria (Say). Gainesville, Fla., Sept. 26-Oct. 2, (Mutchler and Watson). Lake Okeechobee, Fla., May 2, Crescent City, Fla., April 23 (Van Duzee Coll.).

Cicadella marathonensis, new species

Large, broad; length, 6.5 mm.; width across eyes and hemelytra, 2 mm. Head short; anterior margin of vertex nearly continuous with outside margins of eyes. Transverse arcs on the front numerous and slightly raised. Vertex about half the length of pronotum, and its length less than half its width between the eyes at the base; surface finely punctured. Face, as seen from the side, moderately convex; clypeus straight and continuous with the profile of the face. Pronotum transversely sculptured with irregular, slight indentations. Scutellum with a slight transverse depression. Anterior tibiæ simple. Hemelytra long and broad, but not entirely covering the lateral margin of abdominal tergum.

Vertex, anterior part of pronotum, and scutellum, yellow marked with black; remaining part of pronotum, bluish-gray marked with irregular black blotches unevenly scattered. Markings of vertex as follows: an apical triangular spot; a short distance on each side of this an irregular vitta running parallel with the triangle and nearly meeting its mate just in front of the center of vertex, then turning outwards to a little in front of ocellus, where it joins a large spot; two semi-quadrate spots evenly spaced between the ocelli; a triangular spot at the base below each ocellus; a short line in center at base; a spot between each ocellus and eye but close to the ocellus; in front of each of the last-named spots an irregular vitta continuing down along the suture of face and antennal ledge. On the face there are two dark brown, irregular vittæ, somewhat interrupted here and there, running down across the disk, starting obliquely at the edge of vertex (nearly reaching the markings above but not connected), then parallel to near the clypeus. Clypeus marked with a central, brown vitta. Rostrum dark brown and slightly hairy. Pronotum marked with irregular, unsymmetrical, black spots and blotches. Scutellum with two longi-

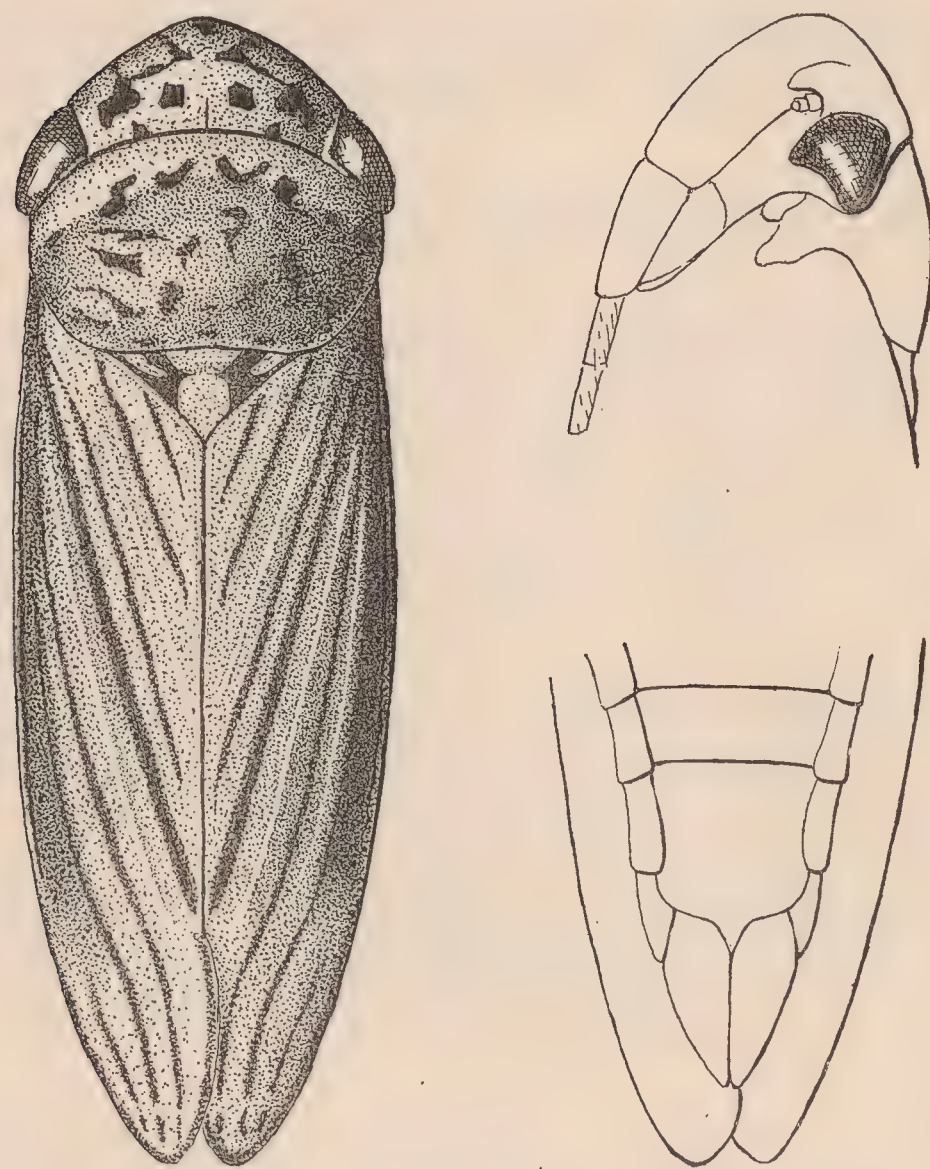


Fig. 1. *Cicadella marathonensis*, new species. $\times 12$.

tudinal, black bars, constricted at the scutellar depression. Hemelytra gray; veins pale, indistinct or white; costal margin of corium pale; a jet black subcostal stripe commencing a short distance from the base and ending just before the membrane; parallel with this stripe is a broad sanguineous vitta commencing at the base and fading out at the membrane, half of its width lying in the outer anteapical cell. Costal margin of membrane marked with a brown border; all the cells of the hemelytra, except the outer and inner apical, are adorned with a brown stripe; these stripes have a tendency to be interrupted where they pass over cross nervures between the apical and anteapical cells; claval suture deep and strongly bordered with brown. Wings: apical area, milky white; basal area, black somewhat blending with the white of the apical area; veins, jet black. Abdomen, black above; lateral edge, yellow and partly exposed. Venter, yellowish-gray, mottled with brown. Legs, a dirty yellowish-gray. Pectoral pieces and abdomen, scantily pruinose in places.

Genitalia: female segment as long as pygofer, broad, keeled and terminating in an acute point.

Described from one female collected by Dr. F. E. Lutz at Marathon, Texas, July 1, 1916.

Type in collection of American Museum of Natural History.

This species is readily separated from our other *Cicadella* by its robust appearance and shape of vertex. It comes very close to the genus *Kolla* Distant, its line of vertex being nearly continuous with the outside margins of the eyes, but, as will be seen in Fig. 1, there is a slight indentation between

these. Furthermore, the eyes and line of vertex are both slightly convex, and the vertex is not foveate as in *Kolla*. On the other hand, it is quite an unusual *Cicadella* with its short and broad vertex sloping and gently merging with the line of face, forming a rather graceful curve instead of an angle at the apex of head as is usual with our species of this genus. However, there seems to be no better place for it.

Kolla bifida (Say). Ramsey, N. J., Aug. (Lutz). Paterson, N. J., July (Grossbeck). Lake George, N. Y., Aug. 19; Clayton, Mass., Sept. 10 (Zabriskie Coll.). Valley of Black Mts., N. C., June 20–Aug. 31, and Black Mts., N. C., June–Sept. (Beutenmüller).

Kolla bifida* var. *fasciata (Walker). Gainesville, Fla., Sept. 26–Oct. 2; Monticello, Fla., Oct. 4–8 (Mutchler and Watson). Lakeland, Fla., May 8, and Ft. Myers, Fla., March 30 (Grossbeck). La Belle, Fla., Nov. 14 (Lutz). Crescent City, Fla., April 24 (Van Duzee Coll.).

Kolla geometrica (Signoret). Monticello, Fla., Oct. 4–8; Gainesville, Fla., Sept. 26–Oct. 2 (Mutchler and Watson). Sanford, Fla., April 28; Crescent City, Fla., April 23 (Van Duzee Coll.).

Kolla hartii (Ball). La Belle, Fla., Nov. 14; Fort Myers, Fla., Nov. 13 (Lutz). Sanford, Fla., April 28 (Van Duzee Coll.). Pensacola, Fla., Oct. 11–14 (Mutchler and Watson).

Kolla similis (Walker). Miami, Fla., Nov. 5 (Lutz). Panama, R. P., Feb.–March. San Jose, Costa Rica, March.

Helochara communis Fitch. Tompkins Cove, N. Y., Sept. 13 (Lutz). New York, N. Y., June 28 (Southwick Coll.).

Graphocephala coccinea (Forst). Represented by many examples from Massachusetts, New York, New Jersey, and North Carolina. Sanford, Fla., April 4–26 (Van Duzee).

Graphocephala versuta (Say). Valley of Black Mts., N. C., Aug. 31; Black Mts., N. C., July–Sept. (Beutenmüller). Sanford, Fla., April 26 (Van Duzee Coll.). Monticello, Fla., Oct. 4–8, and Gainesville, Fla., Sept. 26–Oct. 2 (Mutchler and Watson).

Dræculacephala floridana Ball. Everglade, Fla., April 11–15 (Grossbeck).

Dræculacephala 7-guttata (Walker). Sanford, Fla., May 3 (Van Duzee Coll.). Titusville, Fla., Nov. 8 (Lutz). Monticello, Fla., Oct. 4–8, and Pensacola, Fla., Oct. 11–14 (Mutchler and Watson).

Dræculacephala balli Van Duzee. Monticello, Fla., Oct. 4–8 (Mutchler and Watson). This species was recently described from Georgia, and has not hitherto been recorded from elsewhere.

Dræculacephala bradleyi Van Duzee. Ft. Myers, Fla., March 30 (Grossbeck). Crescent City, Fla., April 24; Sanford, Fla., April 26 (Van

Duzee). Lakeland, Fla., Nov. 10 (Lutz). Like the preceding species, this was described and recorded only from Georgia. Both species have been confused with *D. minor*.

Dræculacephala angulifera (Walker). Represented by many examples from New York, New Jersey, and Florida. Nome, Texas, June 30, and New Orleans, La., June 29 (Lutz). These were all placed with *D. mollipes*.

Dræculacephala mollipes (Say). Common from Massachusetts, Connecticut, New York, New Jersey, and North Carolina.

Dræculacephala minor (Walker). Pine Island, N. Y., Sept. 8 (Lutz). Sanford, Fla., May 3 (Van Duzee Coll.). Phoenix, Ariz. (Kunze Coll.). California (Edwards Coll.). The Pine Island record is an exceedingly northern one.

Dræculacephala inscripta Van Duzee. Fort Lee Dist., New Jersey, July 13. Recently described from one female taken in Georgia. This is the first record of its occurrence in New Jersey.

Dræculacephala manitobiana Ball. Spruce Brook, Newfoundland, Aug. 8 (Leng).

Dræculacephala noveboracensis (Fitch). Great Piece Meadow, N. J., Aug. 5; Ramsey, N. J.; Carmel, N. Y., Aug. 13 (Lutz). Wyandanch, L. I., N. Y., Aug. 21 (Olsen).

Dræculacephala reticulata (Signoret). New Orleans, La., June 29 (Lutz). Numerous examples from Florida.

Pagaronia tripunctata (Fitch). Valley of Black Mts., N. C., June 21-Aug. 30 (Beutenmüller).

Eucanthus acuminatus (Fabricius). Black Mts., N. C., June (Beutenmüller).

Article II.—THE EXTERNAL CHARACTERS, SKELETAL
MUSCLES, AND PERIPHERAL NERVES OF *KOGIA*
BREVICEPS (BLAINVILLE)

BY H. VON W. SCHULTE AND M. DE FOREST SMITH

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INTRODUCTION

The foetal *Kogia* [Physeteridæ; Odontoceti] described in this paper was taken from a large female which became stranded at Long Beach, Long Island, the skeleton of which is preserved in the American Museum of Natural History, No. 36595.

The specimen was entrusted to us for study by Dr. J. A. Allen, at the suggestion of Mr. R. C. Andrews. To both of these gentlemen we would express our sincere gratitude. We would also express our appreciation to Mrs. Helen Ziska for her painstaking skill in the preparation of the illustrations.

The foetus, which is a male, was preserved in alcohol and received in good condition. The muscles were rather soft but not to such a degree as seriously to interfere with dissection. The cheeks, however, especially the left, had pressed against the side of the container and had desiccated. On the left side, the underlying muscles could not be studied; on the right, with only partial success. It was also impossible to find on the surface the orifice of the ear and the location of hairs; the situation of these structures was ascertained only during the removal of the blubber.

While the writers have collaborated throughout in the study of this *Kogia*, one of them (Smith) has charged himself especially with the nerves, the other with the muscles, and each would assume in his division of the work the major responsibility for the statements made therein.

MEASUREMENTS

The dimensions of this specimen are given in the accompanying table:—

	cm.
Total length — notch in flukes to snout.....	109.7
Tip of snout to eye.....	Left, 15 cm.; Right, 16.0
“ “ “ “ blow hole.....	10.5
“ “ “ “ axilla R.....	25.5
“ “ “ “ axilla L.....	27.0
Notch in flukes to anus.....	36.0
“ “ “ “ preputial orifice.....	60.5
“ “ “ “ dorsal hump.....	47.3
“ “ “ “ umbilicus.....	63.3
Flukes — tip to tip.....	21.0
Depth of pedicle just anterior to flukes.....	7.1
“ “ “ midway between flukes and anus.....	12.7
Fin tip to head of humerus, R.....	18.7
“ “ “ “ “ L.....	19.3
“ “ to anterior insertion, R.....	19.0
“ “ “ “ “ L.....	20.0
“ “ “ posterior “ R.....	14.0
“ “ “ “ “ L.....	14.5
Greatest breadth, R.....	6.5
“ “ L.....	6.5
Length of blow hole.....	2.4
Circumference at eye.....	58.0
“ at axilla.....	62.5
“ at umbilicus.....	60.5
“ at anus.....	39.9
“ midway between anus and flukes.....	29.6
“ just anterior to flukes.....	17.0
Length of dorsal fin at base.....	11.5
“ “ “ “ to incisure.....	9.8
Height of dorsal fin.....	5.2

EXTERNAL CHARACTERS

Coloration. The dorsal parts are glossy black; the ventral, a dirty buff color, apparently altered in hue by the preservative. The light area includes the throat, the under side of the flippers, and the venter; extending about half-way up the trunk immediately behind the axillæ and contracting gradually towards the pedicle it is continued as a narrow strip to the flukes, the under parts of which are also light colored. The margins, as well as the

dorsum, of flippers and flukes are dark, and the pigmentation encroaches to a slight degree upon their under sides.

Contour. In the illustrations of the adult specimens of *Kogia*, the snout projects strongly beyond the mouth. In le Danois' figure, its contour ascends at an angle of about 45° to the level of the eye and then turns at something less than a right angle into the sloping convexity of the head. In his sections, this contour is seen to follow closely the outline of the spermaceti organ. The large size of this structure in the adult would seem, therefore, to determine the difference in the shape of the snout as compared to the foetus, for in the specimen here described the snout ascends with only a slight deviation forward from the vertical. Its tip is separated dorsally by a concavity — probably artificial — from the convexity of the spiracular sac. Beyond this again is a slight incurvation of the outline followed by a second convexity at the insertion of the dorsal muscles into the occipital



Fig. 1. Contour of foetus at term.

bone. Thence to the pedicle the contour is evenly and slightly arched, the hump occupying the summit of the curve. At the beginning of the pedicle, a shallow concavity is present, beyond which the contour is again slightly arched, finally descending to the flukes with a steep slope. In this respect and indeed in its whole dorsal outline, with the exception of the hump it resembles Krefft's wood cut far more closely than either of Owen's figures. The ventral contour is uniformly and very moderately convex, save for slight concavities at the throat, at the preputial orifice, and at the junction of the pedicle with the trunk. The first two are indicated in Owen's illustrations, but in them the protrusion of belly and chest are much greater. It will be remembered that the specimen from which they were taken was a pregnant female.

The head. The head is described by le Danois as conical. In this younger specimen it is rather to be described as wedge-shaped. The sloping sides meet in a line ascending from the mouth like the stem of a boat.

The blow-hole, lunate with caudally directed horns, is situated in the

space between the eyes about as in Owen's figure and not as far rostrad as in le Danois', with which however it corresponds in position with reference to the median line.

The asymmetry of the head is also shown in the position of the eyes, the left being visibly nearer the tip of the snout, as le Danois has pointed out.

To the description of the mouth by this last named writer, our material enables us to add little. The sulcus corresponding to the mandibular teeth is situated at the junction of the lip and rostrum. It is wide and shallow and not yet divided into pits for the teeth — an adult condition recorded first by Wall. Krefft failed to find the pits, but they were again observed by le Danois. The lower teeth are present as a close-set series of elevations but have not yet broken through. They are blunt and rounded, fifteen in number; the largest at the middle of the series; the last three are very small.

In the midline of the palate, at its rostral extremity close to the sulcus of the upper lip, is a distinct ridge 15 mm. in length. No pits were found in its vicinity. It is probable, however, that it represents the papilla incisiva. There is no external evidence of premaxillary teeth, nor were we able to discern their anlagen in the dissection of the contents of the alveolar sulci of the maxilla. Further, we found no trace of Benham's sclerite. The condition of the soft parts is not such as to warrant an absolute statement, but good enough for us to feel that had these structures attained even a moderate size they would have been observable.

The flipper. The pectoral limbs are short and broad, with a robust preaxial margin. Their thickness diminishes towards the postaxial border, which is tenuous but even. They are broadest in the metacarpal region and thence diminish rapidly, largely at the expense of the postaxial border, which becomes concave. The tip is obscurely recurved.

The hump. The dorsal fin is thick and solid, falcate and prolonged along the back by a low ridge. It is less elevated than in Owen's figure. Krefft represents it as a low irregular ridge.

The pedicle. The pedicle is high and compressed. Demarcated from the trunk by slight concavities in its ventral and dorsal contours, it maintains its size to near the flukes where it diminishes rather abruptly.

The flukes. The flukes are not symmetrical. The greatest transverse measurement of the right is 11.5 cm.; the greatest sagittal, 10.5 cm. The corresponding measurements on the left are 10.5 cm. and 10.6 cm. The right fluke also projects more transversely. Their inclination from the pedicle could not be determined as they had become bent in the container.

The vent. The anus is situated in a depression 18 mm. long by 12 mm. broad, bordered at the sides by thick ridges.

The preputial orifice. The preputial orifice is situated 19 mm. caudal to

the umbilicus. It measures 21 mm. in length by 10 mm. in breadth, and, like the vent, is bordered at the sides by heavy ridges. Just caudad of the opening, there is a slight incurvation of the ventral contour which does not correspond to the extremity of the phallus and is perhaps due to the bending of the foetus in its container.



Fig. 2. Contour of flukes viewed from above.

Hairs. Four hairs, arranged in an oblique line, were present in front of the eye. The intervals between these hairs were such as to suggest that a fifth had disappeared from the middle of the series. None was observable on the surface, which had dried.

MYOLOGY

For the study of the musculature of odontocetes, the fundamental work is that of Stannius upon *Phocæna*,¹ which supersedes the earlier and less detailed study of Rapp,² as well as the scattered notes of Cuvier³ and Meckel.⁴ Murie⁵ has described and beautifully figured conditions as they obtain in *Globicephalus* and has also notes upon *Grampus* and *Lagenorhynchus*. Leche's⁶ compilation is uncritical but useful for reference. A larger number

¹ Stannius, H. Beschreibung der Muskeln des Tümmlers (*Delphinus phocæna*). Müller's Arch., 1849.

² Rapp, W. Die Cetaceen. Stuttgart, Tübingen, 1837.

³ Cuvier, C. Leçons d'anatomie comparée. Paris, 1805.

⁴ Meckel, J. F. System der vergleichenden Anatomie. Halle, 1821-1833.

⁵ Murie, J. *Grampus rissoanus*. Jour. Anat. and Phys., V, 1871. *Lagenorhynchus albirostris*. Jour. Linn. Soc., 1870. On the organization of the Caaing whale, *Globiocephalus melas*. Trans. Zool. Soc. London, VIII, 1874, p. 235.

⁶ Leche, W. Mammalia: Bronn's Thier-Reich. Leipzig, 1874-1900.

of workers have concerned themselves with special muscular complexes and they are referred to in connection with the regions they have recorded.

In the following account of the skeletal muscles of *Kogia*, comparison has been made, where possible, with conditions in other odontocetes, occasionally with mystacetes; but it has been chiefly purposed to describe objectively the arrangements obtaining in this little known whale; for, as yet, only the muscles of the genital tract (Benham,¹ le Danois²) of the larynx (Benham), and of the respiratory passages, head, and neck (le Danois), the last under unfavorable circumstances, have been examined.

Panniculus carnosus. Placed between the superficial and deep layers of blubber, the panniculus forms an extensive investment of the trunk and is continued over the pedicle by a strong aponeurosis. In *Phocæna*, it has been described by Rapp and later by Stannius in much detail. Behind the shoulder, it is clearly differentiated into dorsal and ventral divisions by a fibrous raphe reaching from the flipper to the beginning of the pedicle in the vicinity of the vulva and anus. To this raphe, the fasciculi ascend or descend with an inclination rostrad, and this arrangement apparently obtains generally among odontocetes, *pace* Murie who has described and figured the panniculus of *Globicephalus melas* without a raphe. In the small foetus of that species in our possession, the raphe is present and the panniculus of the trunk conforms strictly to the conditions described by Stannius in *Phocæna* and observed by us in *Kogia* and *Tursiops*. In the post-axillary region, therefore, uniformity prevails in this muscle among the cetaceans hitherto studied, inclusive of the mystacetes *Balænoptera* and *Megaptera*.³ Ventrally in all, the muscles of the two sides are separated by fibrous tissue as far as the sternum, the fasciculi becoming continuous from side to side in the neck and intermandibular region.

In the region of the pectoral limb and rostrad, the arrangement becomes somewhat complicated from the acquisition on the part of the panniculus of attachments to the flipper, to the maxilla, and to the cranium, and, further, by the development of interruptions in the sheet both ventrally over the pectoralis and dorsally at the shoulder. Because of the differences in detail of these arrangements, it will be convenient to follow the accounts of the several genera separately.

In *Phocæna*, the dorsal division forms a continuous sheet from occiput to the region of the genitalia. Rapp and Stannius describe no disturbance

¹ Benham, W. B. On the larynx of certain whales (*Cogia*, *Balænoptera*, *Ziphius*). Proc. Zool. Soc. London, 1901. On the anatomy of *Cogia breviceps*. Proc. Zool. Soc. London, 1901.

² le Danois, E. Recherches sur l'anatomie de la tête de *Kogia breviceps* Blainv. Arch. de Zool. exp. et gen., (5), VI, 1910. Recherches sur les viscères et le squelette de *Kogia breviceps* Blainv. *Idem.*, VI, 1911.

³ Mem. Amer. Mus. Nat. Hist., N. S., I, part 6, 1916.

of the uniform ventro-rostral course of its fasciculi at the shoulder, except only (Stannius) a moderate concentration over the scapula, and this implicitly rather than explicitly as a necessary consequence of the direction given the bundles of occipital origin. These descend with a caudal inclination to the side of the neck and then sweep transversely into continuity with the ventral division. It is fair to suppose that the inclination of the fasciculi changes from ventral and rostral to directly ventral in the region of the limb girdle, without interruption of the continuity of the sheet, and therefore with some concentration of the bundles acting upon the limb.

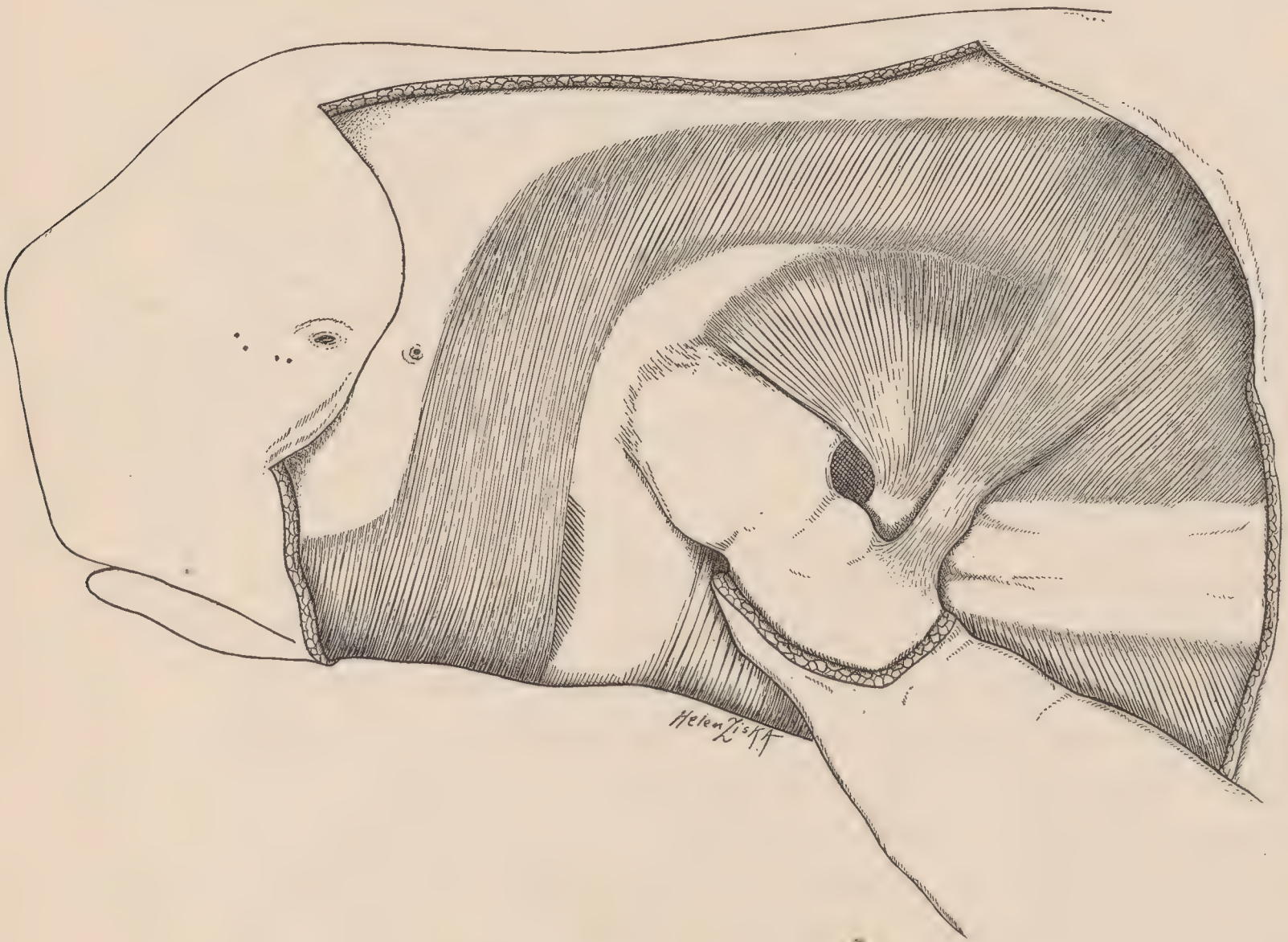


Fig. 3. Panniculus carnosus.

They are inserted into the aponeurosis upon the lateral surface of the flipper and into the corresponding surface of the humerus. The ventral division passes without interruption over the thorax and neck into the intermandibular region. A small area of sternum is exposed between the muscles of the two sides, beyond which their fasciculi are directly continuous across the median line. Those of the chest insert into the fibrous investment of the flipper. Those of the neck are continuous dorsad with the fasciculi of occipital origin previously mentioned; and, finally, those of the intermandibular region stretch transversely between the mandibles. The panniculus extends continuously over the pectoralis major and has no inti-

mate connections with that muscle. We find no justification for Stannius' statement that Rapp designated any portion of panniculus as pectoralis major or that his account differed from Stannius' own save in its omission of details.

In *Tursiops*, the ventral divisions are separated by a broad median aponeurosis except at the vulva where the muscular fasciculi are prolonged to the sides of the vagina and also to the rectum. The fasciculi are directed dorsad and rostrad to the raphe, overlapping to a very slight degree the caudal margin of the pectoralis major. Otherwise, this latter muscle is exposed in its whole extent, the thoracic portion of the panniculus defaulting in the whole region of the greater pectoral. In the neck a triangular aponeurosis is present between the pannicular fasciculi of the two sides. Its base corresponds to the rostral margin of the pectoral; its apex lies in the transverse plane of the auditory orifices. Beyond it, the fasciculi are continuous from side to side. In the intermandibular region, these are attached laterally to the fibrous structures of the lip, sweeping over the ventral margins of the mandibles, only a few of the deeper bundles gaining an insertion into the lateral surfaces of these bones. Caudal to the angulus oris, some of the bundles ascend to be inserted into the fibrous tissue that covers the masseter. The dorsal division extends from occiput to the region of the vulva, here becoming very narrow. In the region of the shoulder, the fasciculi gradually alter their direction, becoming transverse and ultimately inclined slightly caudad. The most rostral fasciculi terminate in the fascia over the masseter and about the external auditory meatus; those next succeeding pass between the meatus and the shoulder in a broad band, concealing the deep muscles and inserting upon the sides of the aponeurotic triangle in front of the ectopectoral. Between these and the next fasciculi going to the shoulder, a narrow fibrous interval has developed and this broadens ventrad, becoming continuous with the ventral aponeurosis just described. Some such interposition as this would seem necessarily to result from the divergent direction of the fasciculi of the neck and of the shoulder, the former being transverse, the latter inclined caudad; and this would hold true of *Phocæna* as well as of *Tursiops*. In the latter genus, the process has apparently advanced, for the caudally inclined fasciculi converge towards the hinder margin of the flipper close to the insertion of the lateral raphe, instead of being diffusely attached to the aponeurosis of its ectal surface. The effect of this arrangement is to enhance the force of adduction exerted by the panniculus and further to elevate the flipper when closely appressed to the side of the thorax, at the sacrifice of some efficiency in abducting and elevating the extended flipper. With the limb extended, the contraction of these fasciculi would tend to elevate its post-

axial margin and only secondarily produce a general elevation of the limb as a whole.

In *Kogia*, the ventral and dorsal divisions are separated by a broad aponeurosis, which contracts to a raphe only as the axilla is approached. In the ventral midline, an aponeurosis of moderate width separates the muscles of the two sides between the vulva and the ectopectoral. The ventral division in the trunk extends from the beginning of the pedicle just caudal to the anus as far as the pectoralis major, overlapping the abdominal fasciculi of that muscle and inserting in part into the aponeurosis which covers its sternal portion. The great majority of bundles insert into the lateral raphe and aponeurosis; all have an oblique rostro-dorsal direction. There is a wide pectoral interval in the panniculus, which in the neck is prolonged by a median aponeurosis as in *Tursiops*, not triangular as in that form but with a curved rostral border. The intermandibular fasciculi have the same arrangement. The dorsal division extends from opposite the anus, here thin and narrow, to the occiput. The most rostral fasciculi are directed ventrad and caudad to the fascia over the masseter. The next, sweeping ventrad in the neck as a broad band of parallel bundles, arrive at the throat and insert upon the ventral aponeurosis or become continuous with those of the opposite side. This aponeurosis lies in the same plane as the intermandibular fasciculi and forms a caudal continuation of the layer. The portion of the dorsal division related to the flipper is highly modified in the direction of concentration at its axillary margin. The aponeurosis of the neck extends far dorsad in front of the shoulder, intervening between it and the band of fasciculi descending on the side of the neck. From its dorsal extremity, a very narrow arched inscription extends to the axilla where it joins the lateral raphe. The bundles of the panniculus arising from the dorsal aponeurosis insert into this fibrous arcade and in front of it into the prolongation of the gular aponeurosis. Those more caudally placed converge to form a band of muscle, which reaches the lateral raphe opposite the point where the lower sternal bundles of the pectoral also join it. Ventral to the arched inscription is a fan of muscle converging to the axilla. These fasciculi arise from the fibrous arcade interdigitating with those of the main sheet of the panniculus. They are directed ventrad and distinctly caudad; and, as they approach the axilla, they assume a deeper position, coming to be partially overlapped by the muscular band described above and, under cover of it, gaining attachment to the lateral raphe. This applies only to the caudad fasciculi of the fan. The remainder, becoming aponeurotic, are attached to the deep surface of the ectopectoral and the postaxial margin of the flipper. In this respect *Kogia* has advanced upon the conditions observed in *Tursiops*, which, in turn, stands somewhat higher than *Phocaena*.

In *Globicephalus*, Murie describes a panniculus with a wide thoracic interruption. As has been already stated, he describes no lateral raphe and in his illustrations gives throughout a very unusual direction to the fasciculi. Our small foetus¹ was, unfortunately, somewhat dried, which rendered the examination of its muscles difficult. It was possible, however, to ascertain the presence of a raphe and the usual course of fasciculi in both ventral and dorsal divisions. Otherwise, conditions were much the same as in *Tursiops*, with possibly even less concentration of the dorsal division at the axillary margin of the flipper.

The arrangement of the panniculus in mystacetes, to judge by conditions obtaining in rorquals *Balænoptera* and *Megaptera*, is in essentials the same but differs in the neck and ventral pouch as secondarily modified in connection with the development of the throat furrows. The redundant ventral integuments are in need of muscular support which is supplied by the panniculus along with the mylohyoid and a derivative of the infrahyoid musculature. The panniculus is continuous over the pectoralis from the trunk to the intermandibular region, and on the side of the neck the ventral and dorsal divisions, elsewhere united by a raphe, overlap extensively so that the ventral division attains fixation upon the skull and the dorsal is prolonged into the intermandibular region as a superficial layer. The result of these changes is to reinforce the ventral pouch, which permits of the enormous distension of the mouth and by the contractibility of its wall assists in the discharge of the engulfed sea water through the baleen fringes, the minute organisms on which the rorqual feeds being in this way filtered out and retained.

In *Kogia*, the intermandibular portion of the panniculus is innervated by a branch of the facial nerve. The cervical portion receives its supply from the ventral division of the second, third, and fourth cervical nerves. All of these nerves give small branches to the dorsal portion of the panniculus, the branches emerging through the lateral intermuscular septum. In addition, a large trunk, formed by the second with contributions from the third and fourth nerves, supplies the bulk of the panniculus between the ear and the aponeurosis at the rostral border of the pectoralis.

The portion of the dorsal division lying in relation to the scapula and thence caudad is supplied by the cervico-brachial plexus through five or six large branches arising from the long thoracic nerve. These branches radiate dorsad on the ental surface of the muscle, the more dorsal curving around the caudal border of the scapula.

¹ For the privilege of examining this specimen, we would express our appreciation to Mr. R. C. Murphy of the Brooklyn Institute of Arts and Sciences.

The remainder of the panniculus is innervated by a plexus formed of the long thoracic nerve and branches of the thoracic nerves from the first to the eleventh. This plexus is composed of two longitudinal trunks closely connected with each other and lying ental to the lateral raphe of the panniculus. These trunks give off nerves to both dorsal and ventral divisions of the panniculus.

The nerve supply plainly indicates that the panniculus is a superficial derivative of the general trunk musculature to which, in the neck, is added a similar cleavage product of the hyoid bar. In this it agrees with usual mammalian conditions. Quite generally, however, a high development of the panniculus is associated with a corresponding development of epidermal derivatives, hairs or bristles (Weber), and in the Cetacea these are all but totally wanting. Some other explanation of its function must be sought. That it acts powerfully upon the flipper is beyond doubt, but another suggestion lies at hand in its restriction on the trunk to the regions of the body cavities; for it is lacking over the dorsal muscles and in the pedicle. It would seem, therefore, so disposed as to maintain pressure upon these regions and to prevent their distension by the expansion of their air-containing contents as the animal rises from deep water. The same factor may also be of account in connection with the enormous plexuses of the neck. In this connection, passing reference may be made to the great development of the muscles serving as agents of expiration, notably the rectus abdominis and, in the odontocetes, the transversarius superior.

Accessorius group. The sterno-mastoid arises from the manubrium sterni between the areas occupied by the sterno-hyoid and the ectopectoral; the latter muscle overlies its origin. At first slender and tendinous on its surface, it lies in a groove in the lateral portion of the sterno-hyoid. Diverging from this muscle, its belly becomes flat and ribbon-like, crosses the neck obliquely, and inserts by a flat tendon into the tympano-mastoid and exoccipital under cover of the masto-humeralis. The latter muscle, also ribbon-like, partially overlaps the sterno-mastoid in the neck. It then passes deeply to the deltoid, under cover of which it is inserted by a cylindrical tendon into the summit of the tuberosity of the humerus. There is no trapezius.

These muscles are supplied by nerves which come directly from the trunk of the vagus, probably containing fibers of accessory origin. No communications with the cervical nerves were found.

These muscles are much as in *Phocæna* and agree with the accounts of Cuvier, Meckel, Rapp and Stannius, save that the accessory slip of the last investigator from the hyoid to the sterno-mastoid is not present. Meckel describes a second, partially independent head of the sterno-mastoid,

which Murie believes represents the cleido-mastoid. In *Globicephalus* the muscle is single. None of these authors describe a trapezius, although both Meckel and Murie consider the possibility of so designating the rhomboideus capitis, an interpretation excluded by its nerve supply.

Trachelo-costo-scapular muscles. This sheet is reduced and there is a wide interval between the small levator and the very moderately developed serratus. The levator anguli scapulæ arises from the extremity of the transverse process of the atlas and from the sheath of the scalenus posticus to which it is broadly adherent. The small flat belly turns dorsad around the transversarius capitis and, reaching the basis scapulæ, is inserted under cover of the rhomboideus at some distance from the angle. This muscle has a constant disposition with but trifling variations in other cetaceans (Murie) but the muscle of *Kogia* is peculiar in the displacement of its insertion caudad from the angle of the scapula.

The serratus anticus arises from the first three ribs and the fascia of the intervening spaces. On the right side, there is a broad middle digitation to which much smaller ones are added from the first and third ribs. On the left side, the origin on the first rib is minimal and the fasciculi of this origin are not separable from those of the second rib, so that but two digitations are present. The insertion is into the caudal angle of the scapula on its ental surface. In *Globicephalus*, the sheet seems to be complete from atlas to first rib and thence extend far upon the thorax (Murie). In *Phocæna* the muscle is confined to the thorax but extends to the fourth rib (Rapp) or the fifth (Stannius).

The levator anguli scapulæ receives fibres from the second, third, fourth, fifth, and sixth cervical nerves, through two branches. The first, derived from all of these nerves, supplies also the rhomboideus capitis. The second, derived from the fifth and sixth, enters the distal part of the belly. The serratus anticus receives its nerve supply by a branch derived from the seventh and eighth cervical nerves; this branch pierces the scalenus medius, crosses the first rib, and enters the deep surface of the muscle. Thus these muscles retain, in their nerve supply, evidence of the complete sheet of which they are the reduced representatives.

Rhomboids. The rhomboideus is well developed and differentiated into three elements: a rhomboideus capitis, a superficial, and a deep rhomboideus vertebralis. The first two are concentrated at the rostral angle of the scapula; the last inserts along the whole of its base. The rhomboideus capitis arises from the parietal bone close to the supratemporal crest. Its belly is composed of parallel bundles, crosses the splenius capitis superficially, and inserts into the rostral angle of the scapula. From the insertion, tendinous bands are prolonged upon the fascia covering the deltoid. The

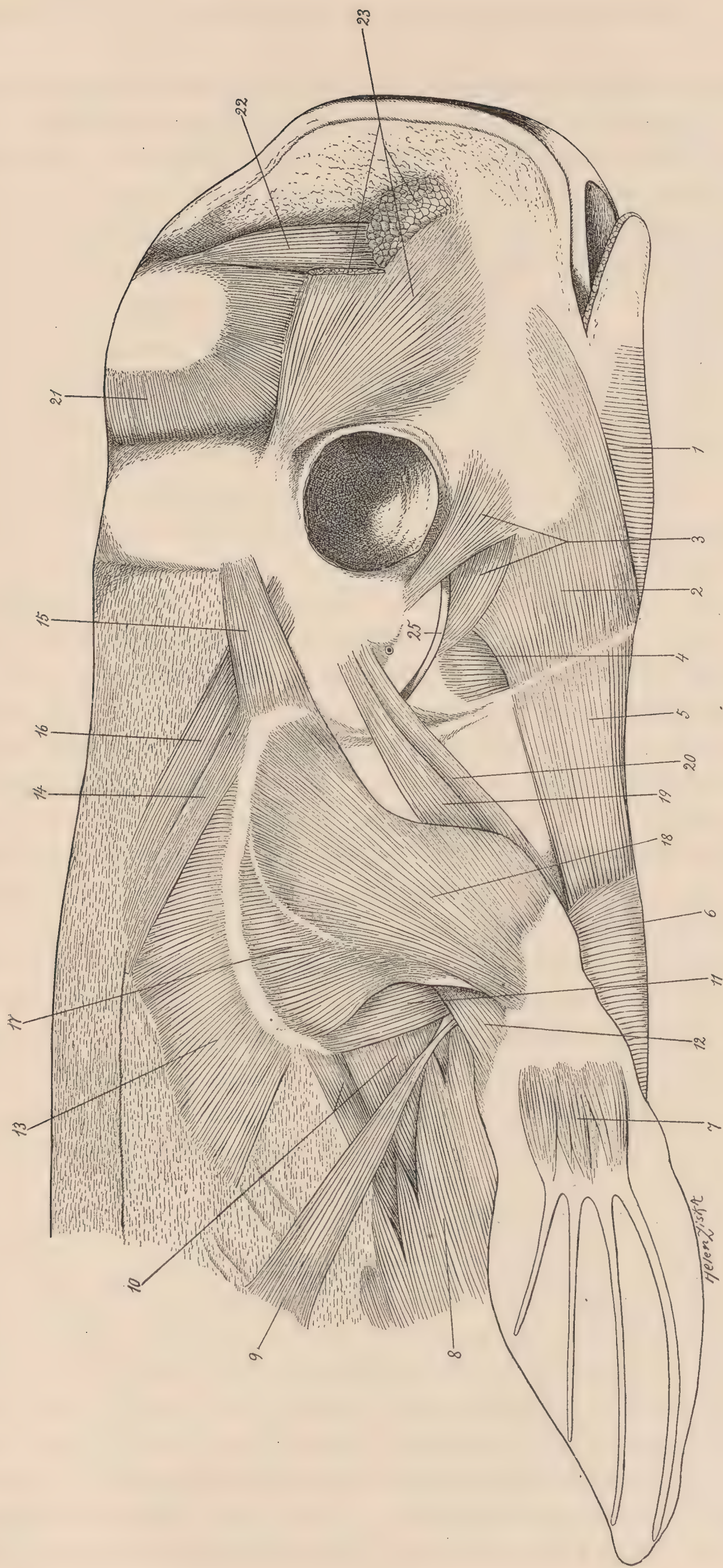


Fig. 4. Muscles of axis and flipper after removal of panniculus.

1, Mylohyoid; 2, Hyomandibularis; 3, Muscular slips innervated by the facial nerve; 4, Depressor mandibulae; 5, Sternohyoid; 6, Pectoralis major; 7, Extensor communis; 8, External oblique; 9, Latissimus dorsi; 10, Serratus anticus; 11, Teres major; 12, Triceps; 13, Rhomboideus vertebralis, deep layer; 14, Rhomboideus vertebralis, superficial layer; 15, Rhomboideus capitis; 16, Splenius; 17, Infrapinatus; 18, Deltoid; 19, Masto-humeralis; 20, Sterno-mastoid; 21, Dilator naris; 22, Retractor; 23, Other facial muscles.

superficial portion of the rhomboideus vertebralis arises from the mid-dorsal intermuscular septum by a strong aponeurosis and inserts into the basis scapulæ close to its rostral angle. Like the rhomboideus capitis, it is prolonged upon the deltoid fascia, but in this case some muscular fasciculi are added to the tendinous bands. The deep layer of the vertebral portion inserts into the whole length of the basis scapulæ, at its rostral angle under cover of the foregoing. Its origin is from the fascia over the transversarius, approaching the lateral intermuscular septum rostrad, where also it is prolonged by tendinous bands in the aponeurosis of the longissimus. On its deep surface, it receives bundles from the third rib over a wide area, less extensively and on a more ventral level from the fourth rib also. Its fasciculi converge to their insertion, the more caudal passing rostro-ventrad, the more rostral nearly transversely. The rhomboideus is subject to variation among odontocetes; or, at least, the accounts of observers differ in important matters. In *Phocæna*, Cuvier, Meckel, and Murie describe a single muscle; Rapp, a superior and inferior coming from the dorsal aponeurosis. Stannius has the origin of the superior extending close to the occipital and its bundles pursuing an oblique caudo-ventral course to the rostral angle of the scapula. The inferior, in addition to its aponeurotic origin, has attachments to the first four ribs. In *Grampus*, Murie noted a rhomboideus capitis "which, indeed, might be a trapezius."

In our *Kogia*, the supply of the rhomboideus superficialis and profundus escaped our observation. The occipital muscle received its supply from the rostral nerve of the levator anguli scapulæ.

Ventro-appendicular muscles. The ectopectoral is a heavy sheet of muscle arising from the linea alba and sheath of the rectus to within 5 cm. of the umbilicus, from the midline of the sternum in its whole length, broadly from the manubrium, and from the cervical fascia over the sterno-mastoid and sterno-hyoid muscles. These last fasciculi would seem equivalent to a pars clavicularis and have a slight caudal inclination in their course to the humerus. The sternal portion is the most strongly developed and has a general transverse direction with but slight tendency to concentration towards its insertion. The pars abdominalis is distinctly thinner and its bundles ascend with a rostral inclination towards the axilla. The insertion is into the neck of the humerus on its flexor surface, into the brachial aponeurosis, and into the deep surface of the lateral raphe of the panniculus. At the caudal border of the muscle on the right side was an additional slip arising from the sheath of the rectus over the cartilages of the fourth and fifth ribs but having no attachment to the cartilages themselves. It soon became tendinous and was inserted into the lateral raphe on the deep surface of the rest of the muscle. It is evidently an element of the pars abdominalis.

The entopectoral is a short, but very robust, muscle of triangular form. It arises fleshy from the lateral angle of the manubrium sterni and from the first costal cartilage; narrowing and becoming mixed with tendinous fibres, it is inserted into the ental surface and tip of the coracoid here fusing with the coraco-brachialis. We found no costo-humeralis such as Rapp and Stannius describe in *Phocæna*. Murie observed this muscle in *Lagenorhynchus* but failed to find it in *Globicephalus*.

The latissimus dorsi is of small size. Its origin, largely by tendinous fibers, is from the sixth and to a less extent the fifth rib and the fascia of the intervening space, approximately midway between the angles and the ventral extremities of the ribs. The flat belly directed rostrad and ventrad passes into a slender tendon which, curving round the teres major, is inserted into the flexor aspect of the shaft of the humerus near the postaxial border. In *Phocæna*, the costal origin is broader, the fourth to the sixth rib (Rapp, Stannius), the sixth to the eighth (Murie); in *Lagenorhynchus*, Murie found it arising from the eighth to the twelfth rib.

The pectoralis major has an extensive nerve supply, apparently receiving filaments from all the cervical nerves except the first. Two loops are formed in the cervico-brachial plexus (Fig. 18) from which numerous branches are given to the muscle. The pectoralis minor is supplied by branches of the great brachial trunk and, in addition, receives a twig from the phrenic nerve. The latissimus dorsi is supplied in common with the teres major by a branch from the great brachial trunk.

Scapulo-humeral muscles. The deltoid has a very large surface of origin from the dorsum scapulæ and from the lateral surface of the huge acromion. On the dorsum, it extends from the rostral border to the infraspinatus and from the base to the neck, here bordering upon the large subdeltoideus. Its origin is extended rostrad upon the prescapular septum intervening between it and the subscapularis, while caudad it overlies the infraspinatus deriving additional fasciculi from its sheath. The acromial portion of the muscle is thickest, the remainder forming a sheet largely aponeurotic on the surface. At the shoulder, the muscle contracts moderately and becomes superficially entirely tendinous, remaining fleshy in its deep layers to its insertion. This is into the preaxial border of the humerus below the tuberosity and into a transverse area on its extensor surface involving the whole width of the bone between the infraspinatus and the origin of the extensor digitorum. Here a strong layer of transverse fibrous bands is applied to the surface of its tendon. There is, further, an extensive aponeurotic sheet prolonged from the tendon into the fascial investment of both brachium and antebrachium.

The muscle is peculiar only in the convexity of its rostral border

occasioned by the very large size of the acromion. Superficially, its fascia is reinforced by tendinous bands continued from the rhomboideus. In this it agrees with *Tursiops* and apparently with *Globicephalus*, to judge from Murie's illustration — a condition which may be considered allied to the fusion of these muscles in *Megaptera*. On the other hand, *Balænoptera* lacks this fusion, and, in the foetus, the rhomboid and deltoid are separated by a narrow area of scapula.

The subdeltoideus, though of large size, is wholly concealed by the deltoid. Its origin, interposed between that of the last named muscle and the infraspinatus, extends to the glenoid margin. The belly crosses the capsule of the shoulder joint, to which it adheres, in contact with the infraspinatus and is inserted between it and the supraspinatus into the tuberosity of the humerus.

The deltoid is, in great part, innervated by the suprascapular nerve but, in addition, receives branches from the circumflex. The subdeltoideus is innervated by branches of the circumflex nerve.

The supraspinatus is small and triangular. Its origin is from the ventral margin of the acromion and from the whole mesal surface of that process, which it occupies with a thin sheet of bundles. Of these, a superficial stratum converge to be inserted into the tip of the coracoid, forming a coraco-acromial muscle in place of the usual ligament which is here represented only by the very thick fascia on the surface of the muscle. This superficial layer is not wholly separable from the rest of the supraspinatus. The muscle narrows as it descends and passes on the rostral aspect of the shoulder joint to the summit of the tuberosity of the humerus where it is inserted between the subdeltoideus and the coraco-brachialis.

The infraspinatus arises from the caudal half of the dorsum scapulæ from the suprascapula to the glenoid margin. The fasciculi from the greater part of this origin converge to an aponeurosis on the free surface of the muscle. This, in turn, contracts to a tendon opposite the shoulder joint and is finally inserted into the diaphysis of the humerus rather nearer its postaxial than its preaxial border and at about the junction of its upper and middle thirds. The fasciculi arising from the ventral third and neck of the scapula have a slightly different arrangement. They are directed ventrad but less distinctly rostrad than the rest of the muscle. In consequence, many of them gain an insertion upon the deep surface of the tendon, and the remainder reach the tuberosity of the humerus directly rostrad of the tendon. This portion of the infraspinatus is wholly concealed by the deltoid.

The supraspinatus is innervated by a branch of the suprascapular nerve; the infraspinatus also receives a branch from this source.

The subscapularis occupies the venter of the scapula but extends upon the suprascapula only rostrad. Its belly is partially divided into slips. Three of these are well defined and constitute somewhat less than half the muscle. The caudal portion forms a sheet in which, towards the shoulder, numerous narrow septa appear and, broadening, cover the surface with a wide aponeurosis. The muscle adheres to the capsule of the shoulder joint, but, as in other cetacea, there is no bursa. The insertion is effected by mixed tendinous and fleshy fasciculi into the distal part of the tuberosity of the humerus on its flexor aspect. The muscle is supplied by several small branches from the lateral cord, from the lesser brachial trunk, and from the intermediate cord of the brachial plexus.

The teres major arises from the whole length of the caudal border of the capsule. It is a broad, thick muscle of parallel fasciculi directed ventrad and very slightly rostrad to be inserted, in common with the latissimus dorsi, into the flexor aspect of the shaft of the humerus between the subscapularis and the origin of the short head of the triceps. It is innervated by a single large nerve arising from the ectal surface of the great brachial trunk.

Coraco-humeral muscles. The coraco-brachialis arises from the mesial surface of the coracoid process, except for a small area at the tip which serves for the insertion of the entopectoral. Its belly is interposed between the supraspinatus and the subscapularis; somewhat adherent to the latter, it is separated from the former by a thick intermuscular septum. This septum, extending from the ventral margin of the coracoid to the tuberosity of the humerus, is firmly attached to the capsule of the shoulder joint, to which it acts as a strengthening band and, in the dissected part at any rate, serves to limit internal rotation of the abducted flipper. The insertion of the coraco-brachialis is into the summit of the tuberosity of the humerus between the subscapularis and the supraspinatus. Its innervation was not found.

The triceps is distinctly more muscular than in *Phocæna* (according to Stannius), although its substance contains an admixture of fibrous tissue. The scapular head is of considerable size and arises from the postglenoid tubercle and adjacent caudal margin of that bone; it is inserted into the olecranon and, in addition, by a fibrous expansion into the aponeurosis of the flipper. A small humeral head is also present. It arises from the postaxial margin of the humerus and inserts upon the olecranon. It is all but wholly embedded in the scapular head, from which it is only imperfectly separable. There is, however, no doubt of the humeral origin of some fasciculi. Murie has recorded the absence of this element in *Phocæna*, *Grampus* and *Lagenorhynchus*; on the other hand, Carte and MacAlister recognized three heads in *Balænoptera*.

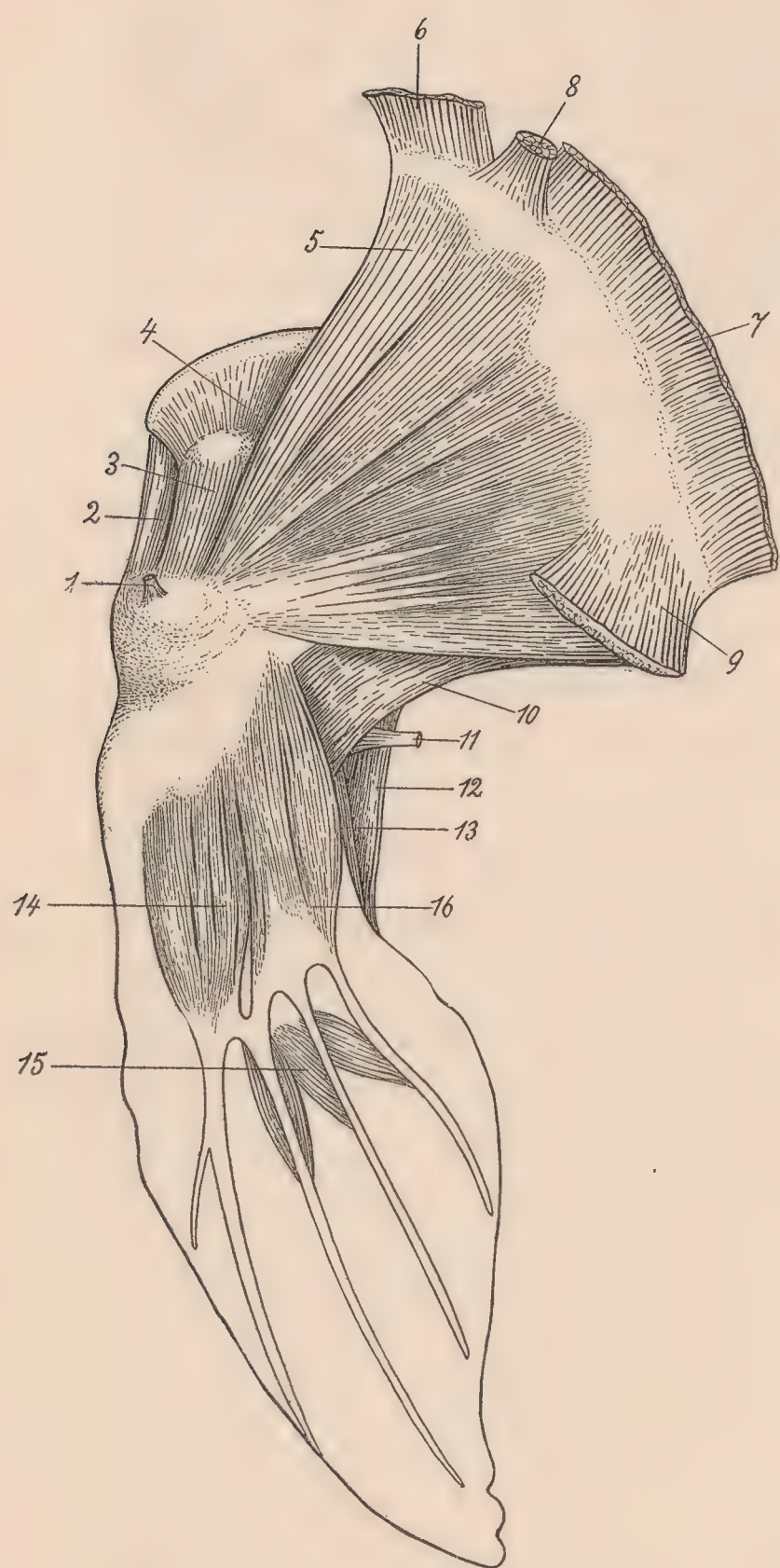


Fig. 5.

Fig. 5. Muscles of right flipper; mesal view.

1, Masto-humeralis; 2, Supraspinatus; 3, Coraco-brachialis; 4, Coraco-acromialis; 5, Subscapularis; 6, Rhomboideus capitis; 7, Rhomboideus vertebralis; 8, Levator scapulæ; 9, Serratus anticus; 10, Teres major; 11, Latissimus dorsi; 12, Triceps; 13, Flexor carpi ulnaris; 14, Flexor digitorum radialis; 15, Interossei; 16, Flexor digitorum ulnaris.

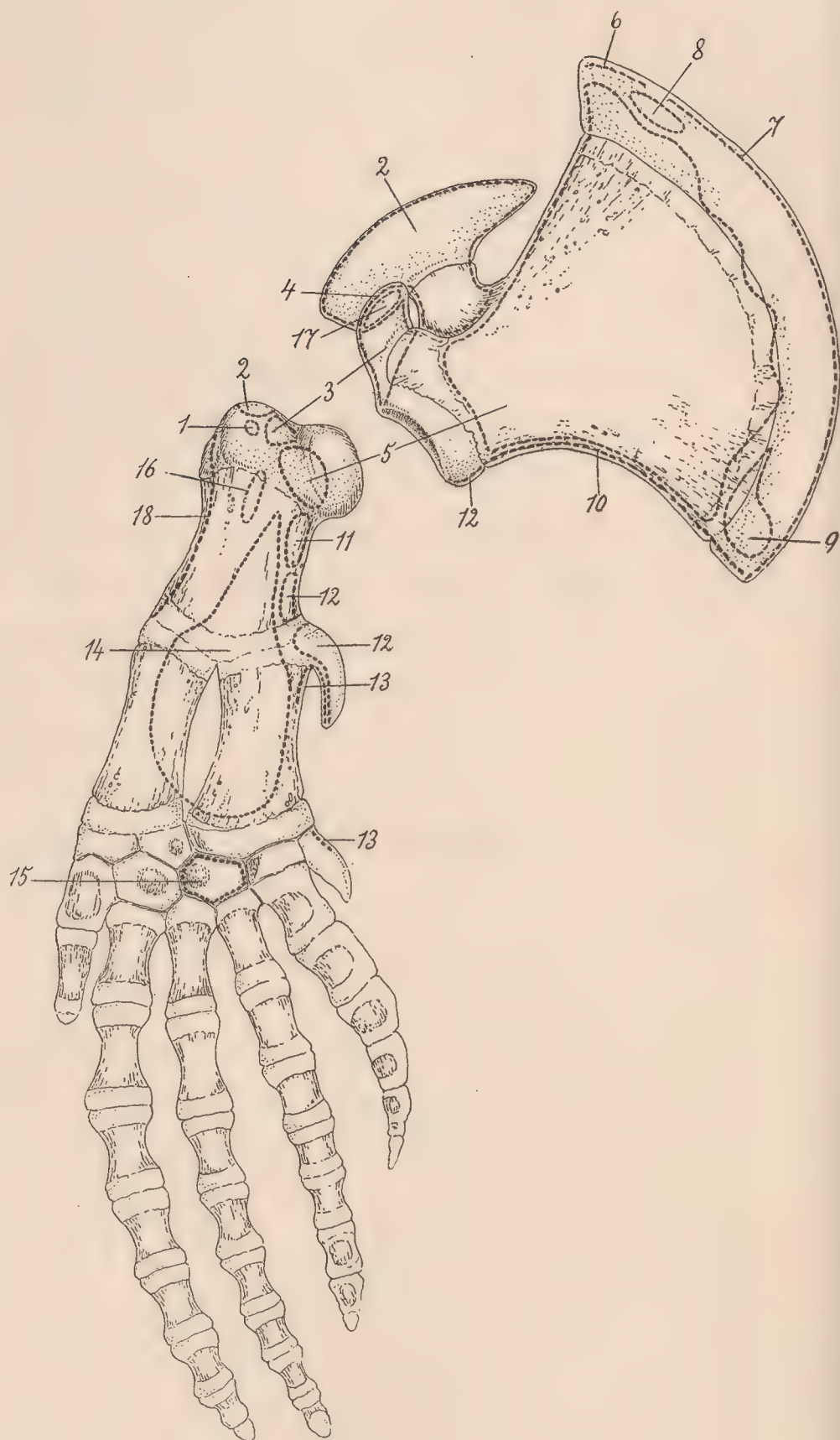


Fig. 6.

Fig. 6. Skeleton of right flipper; mesal view, showing attachments of muscles.

1, Masto-humeralis; 2, Supraspinatus; 3, Coraco-brachialis; 4, Coraco-acromialis; 5, Subscapularis; 6, Rhomboideus capitis; 7, Rhomboideus vertebralis; 8, Levator anguli scapulæ; 9, Serratus anticus; 10, Teres major; 11, T. major and latissimus insertion; 12, Triceps; 13, Flexor carpi ulnaris; 14, Flexor digitorum; 15, Interossei; 16, Pectoralis major; 17, Pectoralis minor; 18, Deltoid.

The triceps receives its nerve supply from the musculospiral nerve as it passes through the substance of the muscle to reach the extensor surface of the flipper.

Intrinsic muscles of the flipper. On the extensor aspect, there is only an extensor communis digitorum. This muscle has an extensive origin from both bones of the forearm and extends proximad upon the lower extremity of the humerus and the fibrous tissue about the elbow joint.

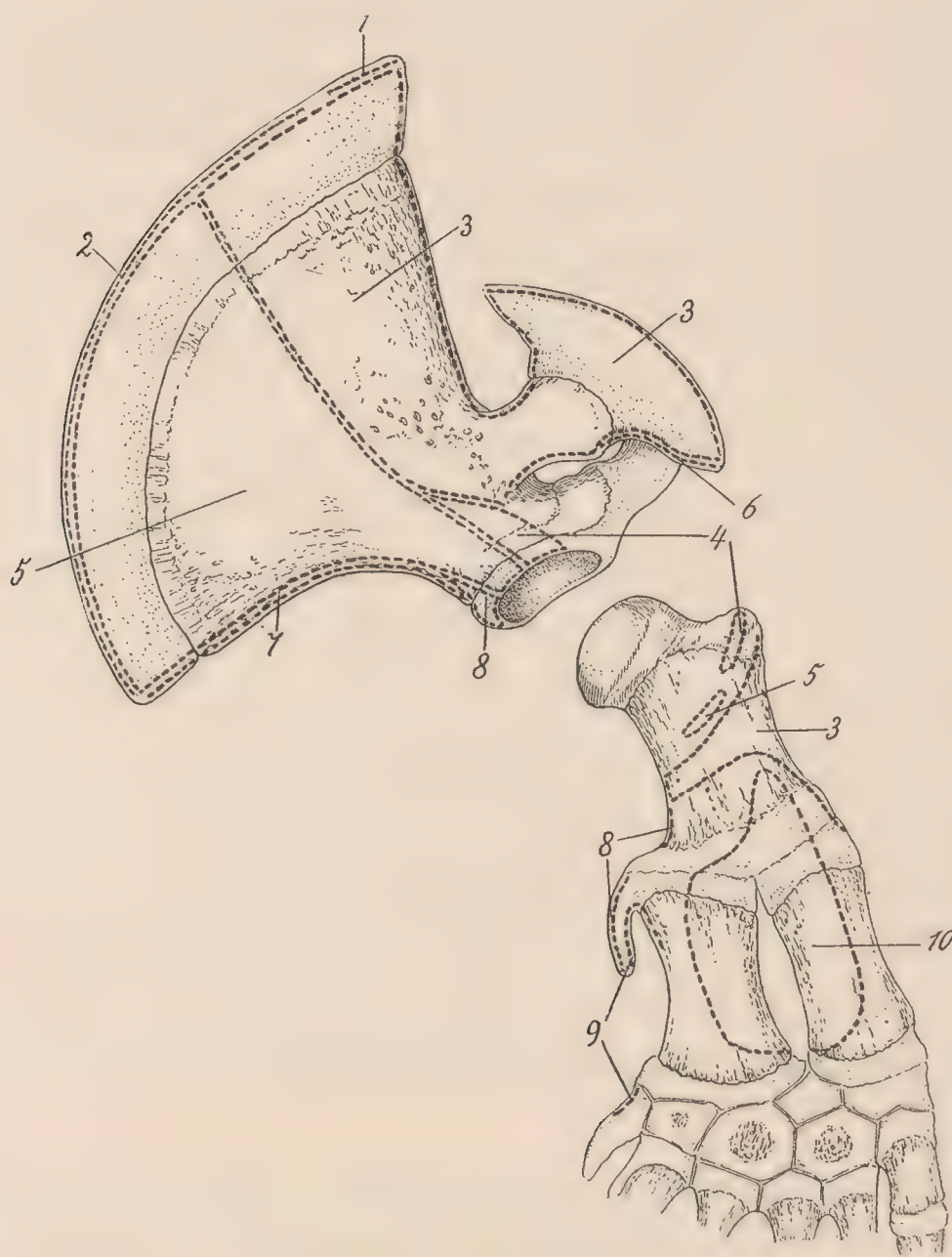


Fig. 7. Skeleton of flipper; lateral view, showing attachments of muscles.

1, Rhomboideus capitis; 2, Rhomboideus vertebralis; 3, Deltoid; 4, Subdeltoideus; 5, Infraspinatus; 6, Supraspinatus; 7, Teres major; 8, Triceps; 9, Flexor carpi ulnaris; 10, Extensor communis digitorum.

On the ulna and radius, the muscle arises from the whole length of the diaphysis, stopping as the distal epiphyses are reached. It also arises from the whole interosseus membrane. In the region of the carpus, four large tendons emerge from the belly and run to the terminal phalanges along the II, III, IV, and V digits. There is no slip to digit I. In their course, they are contained in fibrous sheaths with synovial linings and each tendon follows the axial line of its digit. In the case of the tendon of digit II, this is true only of its proximal portion; distad, it inclines to the

postaxial aspect of its digit sending strong expansions across the phalanges to be inserted into their preaxial borders. These insertions by slips are present also in the other tendons; in the case of digit III, also, they are inserted into the preaxial margins of the phalanges; in digits IV and V, into the postaxial. No slips were found either to carpus or metacarpals. The belly of the muscle is of somewhat complicated structure, being traversed by fibrous septa which partially divide it longitudinally. In this way, the portion of radial origin is separated from the remainder coming from interosseus membrane and ulna. Its fasciculi pass entirely into the tendon of digit II. The fasciculi of ulnar origin are less completely independent and pass to digit V. The remainder of the muscle is partially overlapped by the radial and ulnar portions and sends its fasciculi mainly into two middle tendons with, however, a very considerable muscular contribution to the second digit. Such a muscular slip from the interosseous origin to the tendon of the fifth digit was not found on either side. The extensor muscle is innervated by branches of the musculo-spiral nerve.

The flexor digitorum ulnaris (profundus) is a large muscle, its insertion extending upon the humerus ventral to the insertion of the teres major. It arises further from the fibrous structures about the elbow joint and from the whole length of the diaphysis of the ulna together with the adjacent interosseous membrane. Its belly is imperfectly divided by a longitudinal fibrous septum. The preaxial belly becomes aponeurotic at the level of the carpus and the bundles of the second belly are attached to the postaxial border of its tendon, which then divides into three subequal slips for the third, fourth, and fifth digits. The humeral attachment seems slightly larger than in *Hyperoödon*, where Struthers found it only slightly overlapping the teres.

The flexor digitorum radialis is somewhat smaller than the ulnar flexor, especially in the extension of its origin upon the humerus. It arises from the diaphysis of the radius in its whole length and from the interosseous membrane. The latter portion is coarsely fasciculated by longitudinal, fibrous septa. At the carpus it becomes tendinous and, after giving a slip to the tendon of the third digit, it continues along the axis of the second. As this tendon passes the carpo-metacarpal articulation it gave off a slip of moderate size to the first digit which was inserted upon its metacarpal and its first phalanx. This slip corresponds obviously to the slip in *Hyperoödon*, which has a more distal insertion into the ligament connecting the end of the first digit to the second bone of digit II (Struthers).

The flexor carpi ulnaris is very small and covered by the tendinous expansion of the triceps. It arises from the concave border of the olecranon and, to a corresponding degree, from the shaft of the ulna. It is inserted by mixed tendinous and fleshy fibres into the base of the pisiform.

Beneath the flexor tendons, well developed interossei were found. These were three in number and had a common origin from the lateral carpale and adjacent fibrous tissue of the wrist. Their bellies diverged. The preaxial one followed the axis of the third digit; the middle passed obliquely to the fourth; and the postaxial one, almost transversely to the fifth digit. At the distal extremities of their respective metacarpals they severally become tendinous and were inserted into the ends of the third, fourth, and fifth metacarpals, and the volar aspects of the capsules of these metacarpo-phalangeal joints. These insertions were in the axial lines of their digits under cover of the flexor tendons.

The flexor muscles and the interossei are supplied by the ulnar nerve.

The presence of antebrachial muscles was first recorded in a cetacean by Flower¹ in 1865. Since then they have been recognized and described in *Balænoptera*,² *Megaptera*,³ *Balæna*,⁴ *Platanista*,⁵ *Mesoplodon*,⁶ *Hyperoödon*,⁷ and *Globicephalus*.⁸

In the two ziphioids, substantial differences obtain, both in the number of muscles and in the arrangement of their tendons. In *Mesoplodon*, the extensor digitorum is divided into a radialis with tendons for the second and third digits and an ulnaris for the fourth and fifth. The tendon of the index gives off a slip to the margin of the flipper distad of the pollex. The ulnaris tendon of the fourth digit is very peculiar according to Turner's account, dividing into slips which intercommunicate and again subdivide prior to their insertion upon digit IV and the adjacent interdigital connective tissue. On the flexor aspect, there is a flexor carpi ulnaris, and a flexor digitorum ulnaris and radialis. The ulnaris is remarkable for the number of digits which it supplies, for it sends slips to the postaxial four and, in addition,

¹ Flower, W. H. Observations upon a fin-whale (*Physalus antiquorum*, Gray) recently stranded in Pevensey Bay. Proc. Zool. Soc. London, 1865.

² Carte, A. and MacAlister, A. On the anatomy of *Balænoptera rostrata*. Phil. Trans. Roy. Soc. London, CLVIII, 1869. Perrin, J. B. Notes on the anatomy of *Balænoptera rostrata*. Proc. Zool. Soc. London, 1870. Struthers, J. On some points in the anatomy of a great fin-whale (*Balænoptera musculus*). Jour. Anat. and Phys., VI, 1871. Schulte, H. von W. Anatomy of a foetus of *Balænoptera borealis*. Mem. Amer. Mus. Nat. Hist., N. S., I, part 6, 1916.

³ Struthers, J. On some points in the anatomy of *Megaptera longimana*. Jour. Anat. and Phys., XXII, 1887-8.

⁴ Struthers, J. Account of rudimentary finger muscles found in the Greenland right-whale (*Balæna mysticetus*). Jour. Anat. and Phys., XII, 1877.

⁵ Anderson, J. Anatomical and Zoological researches, comprising an account of the zoological results of two Expeditions to Western Yunnan in 1868 and 1875, and a monograph of the two cetacean genera, *Platanista* and *Orcella*. London, I, 1878.

⁶ Turner, W. The anatomy of a second specimen of Sowerby's whale (*Mesoplodon bidens*) from Shetland. Jour. Anat. and Phys., XX, 1885-6.

⁷ Struthers, J. Account of rudimentary finger muscles found in a toothed whale (*Hyperoödon bidens*). Jour. Anat. and Phys., VIII, 1873-5.

⁸ Murie, J. On the organization of the Caaing whale, *Globiocephalus melas*. Trans. Zool. Soc. London, VIII, 1874.

a slip to the margin of the flipper beyond the end of the first digit. The flexor radialis is correspondingly reduced. Its delicate tendon divides into a slip of communication to the tendon of the second digit, a slip to the terminal phalanx of the first, and a slip to the carpus.

In Struther's *Hyperoödon bidens*, there is also a division of the extensor into radial and ulnar muscles. The first has the same disposition as in *Mesoplodon*. The ulnar muscle subdivides into a portion for digit IV and a portion for digit V. The latter, however, gives a slip equal to one-third of its bulk to the tendon of the fourth digit. On the right side, there is an intermediate fleshy slip from the radial muscle, the tendon of which divided to join the tendons of the third and fourth digits. There is also, on this side, a small tendon from the radial belly of the ulnar flexor to the tendon from the ulnar belly to the fourth digit. The flexor digitorum ulnaris and the flexor digitorum radialis are both well developed. The radialis supplies the large tendon for digit II, from which a slip is given to the margin of the flipper beyond the termination of the first digit. The ulnaris is distributed to the third, fourth, and fifth digits. The tendons for the last two have a short, common stem; that for digit III receives a slip from the radialis. The flexor carpi ulnaris, as in *Mesoplodon*, extends simply between the olecranon and pisiform.

There is, then, a substantial agreement between the antebrachial muscles of these ziphioids and *Kogia*, which differs chiefly in the incomplete division of its extensor.

The tendency to retain an independent radial extensor is, however, evident, though less marked than in *Hyperoödon* (Struthers) and *Mesoplodon* for its digital distribution here is less. In these two ziphioids, independence of this belly is effected by means of an intermuscular septum serving as a common origin to both radial and ulnar extensors, and, in this respect, *Kogia* partially conforms. In them, however, the tendons of the second and third digits arise from the radial belly, which in *Kogia* supplies the tendon of digit II, and that not completely. On the other hand, the tendency of the remainder of the extensor mass to separate a muscle for the fifth digit though initiated in *Hyperoödon* is apparently carried further in *Kogia*, for here the fasciculi of ulnar origin are partially separate and have a direction different from those arising from the interosseous membrane.

In all, the flexor carpi ulnaris is practically identical, and this holds true of the flexor digitorum radialis of *Hyperoödon* and *Kogia*, while in respect to the flexor digitorum ulnaris *Mesoplodon* differs more widely from *Hyperoödon* than that genus does from *Kogia*. The variations recorded on the right side of *Hyperoödon* are indicative of the caution necessary in attempting to find specific characters in details of muscular arrangements, especially

in cases where but few specimens are available for comparison. In *Kogia*, the musculature in question is relatively best developed if not most highly specialized, as is shown by the great breadth of the muscles and their extensive humeral origins. The persistence of interossei may be an expression of the same factor. In *Mesoplodon*, the muscles are, in general, least in size and the peculiarities of that form are possibly instances of the common tendency to vary on the part of rudimentary structures.

In *Platanista*, this musculature is highly peculiar. The extensor communis arises only from the ulna and divides into three tendons for digits III, IV, and V. There is but a single digital flexor which arises from both radius and ulna and is distributed to the second, third, and fourth digits, though Anderson thought it possible that minute tendons may also go to the first and fifth. In addition to the usual carpal flexor, there is an extensor carpi ulnaris. Both arise from the olecranon and their fleshy bellies are prolonged upon the phalanges of the fifth digit.

Regarding conditions in Delphinidæ, our knowledge is far from complete. The majority of investigators are silent or record the absence of digital muscles. In *Globicephalus*, Murie found longitudinal bands in the fascia of the flipper which he believed are representative of tendons, but did not ascertain the presence of muscular fasciculi upon the radius and ulna.

It seems permissible to conclude provisionally that a general, great reduction of this musculature has taken place among the Delphinidæ which distinguish them from other known odontocetes. The Physeteridæ seem, in this respect, fairly homogeneous, while *Platanista*, nearer the latter than the former, is yet divergently modified.

Among mystacetes, the Balænopterinæ agree in the presence of a common extensor, ulnar and radial flexors, and an ulnar carpal flexor. The last extends between olecranon and pisiform, as in the Physeteridæ, although it may vary in *Balænoptera*, where Carte and MacAllister found it extending to the fourth metacarpal and Perrin records its insertion into the ulna. The extensor is simple and divides into four digital slips. In *Balænoptera*, the flexor ulnaris supplies the third, fourth, and fifth digits, and sends a contributing slip to the radialis tendon of the second. In *Megaptera*, the tendons of the two muscles unite and the common expansion supplies four subequal slips to the digits. Contrary to what might be inferred from the great size of the flipper, the muscles are distinctly of less development in *Megaptera*. The palmaris longus attributed to *Balænoptera* by Carte and MacAllister and the flexor sublimis of the same genus observed by Perrin have not been found by subsequent observers.

In *Balæna*, the muscles attain a higher development than in other known cetaceans and an extensor carpi ulnaris is present in addition to the

usual complement. It is less developed than in *Platanista* and its tendon, failing to reach the pisiform, is inserted upon the ulna. The flexor carpi ulnaris is smaller than in *Balænoptera* but otherwise not remarkable (Struthers). The extensor communis is subject to some variation. In an adult, Struthers found it dividing opposite the first row of carpals into four slips. In a young male, the digital tendons were given off at different levels before the carpus was reached, and, on the carpus, there was a communicating slip between the middle tendons. There was, further, a small, deep belly of radial origin, the tendon of which joined that of the third digit. This element is perhaps partially equivalent to the middle portion of the extensor of *Kogia*. The ulnar and radial digital flexors communicate by their tendons so that the ulnar supplies about one-tenth of the tendon of digit II; the radial, about the same amount of digit III. The tendons of the fourth and fifth digits belong exclusively to the ulnaris. The flexor radialis is further remarkable for the division of its belly into deep and superficial layers.

This comparison reveals no fundamental differences between the odontocetes and mystacetes in muscles which, from their rudimentary character and small functional value, might perhaps have been expected to reveal phyletic differences. The evidence, such as it is, serves rather to set the Delphinidæ apart from other cetaceans, and to approximate the other known odontocetes with mystacocetes. The less frequent muscles are present in genera of both suborders, the extensor carpi ulnaris in *Kogia* and *Balæna*; and the interossei, while well developed only in *Kogia*, were recognized on microscopic examination by Leboucq¹ in *Balænoptera*.

Facial musculature. For convenience of description, the facial muscles may be divided into an ental group acting upon the blow-hole and an ectal one associated with the cheek and lips. The basis of this division is found in the peculiar modification of the skull, for the ental muscles arise predominately from the great maxillary crest and summit of the tuberosity, encroaching only on the proximal portion of the rostrum, while the ectal group takes origin from the sides of the cranial projections and from the distal portion of the rostrum.

The ental group comprises a dilator naris (M. nasalis, Stannius) and a muscle which is probably to be interpreted as a retractor. The dilator invests the spiracular sac and inserts into the blow-hole, in part fleshy, in part by an aponeurosis. In consequence of the asymmetry of the region, the muscles of the two sides differ in some respects and are best described separately.

¹ Leboucq, H. Recherches sur la morphologie de la main chez les mammifères marins. Arch. de Biol., IX, 1889.

The superficial portion¹ of the right muscle, arising from the maxillary crest and tuberosity in their whole length, is thin, sheet-like, and imperfectly separable into two layers. It receives a strong slip rostrad from the fibrous tissue adjacent to the antorbital notch and from the maxilla immediately in front of the notch. This latter is not divisible into layers but otherwise is perfectly continuous with the rest of the muscle. The most

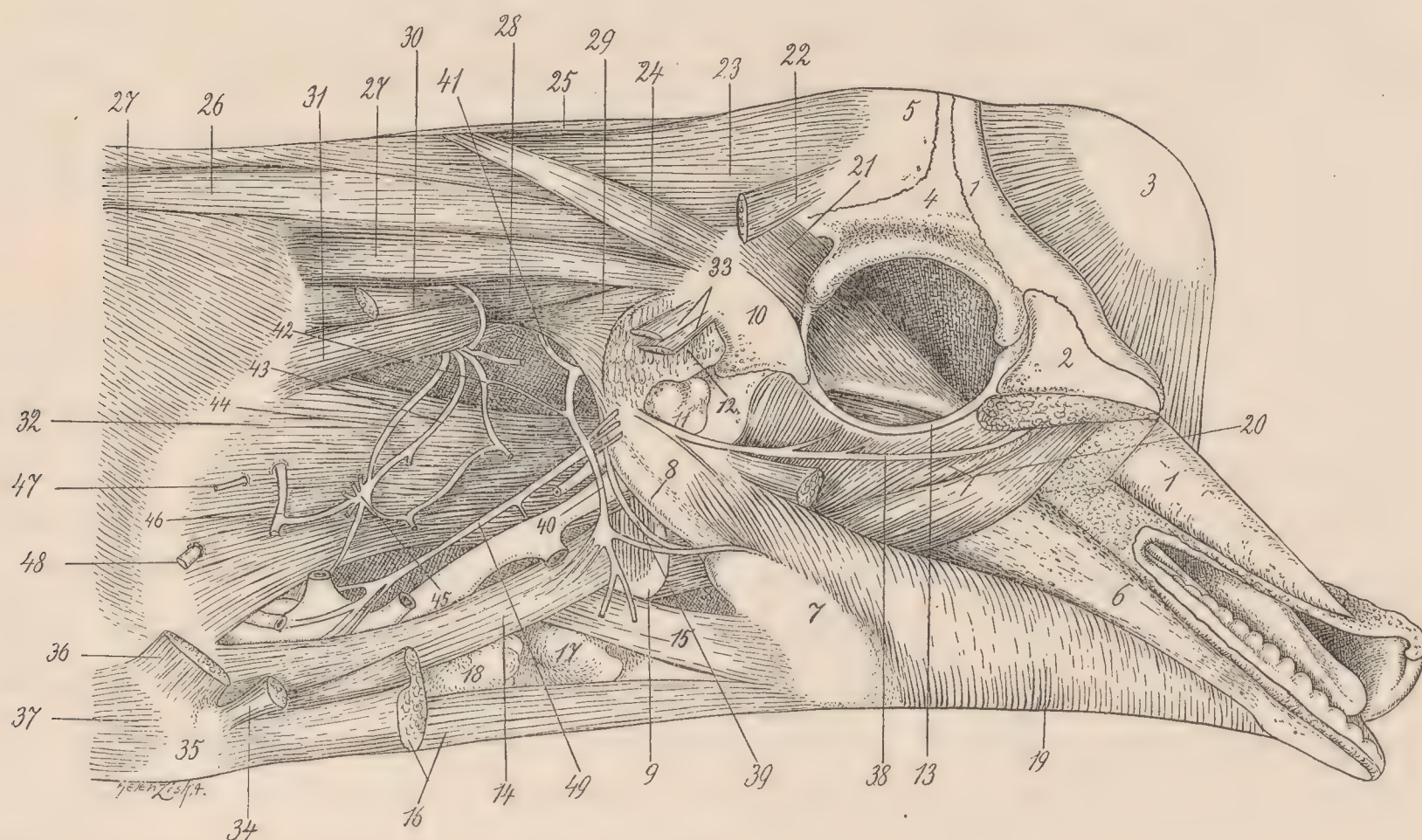


Fig. 8. Deeper muscles of the neck and face.

1, Maxilla; 2, Malar; 3, Spiracular sac; 4, Frontal; 5, Parietal; 6, Mandible; 7, Hyoid body; 8, Stylohyal; 9, Cornu of thyroid; 10, Zygomatic process; 11, Periotic; 12, Tympano-mastoid; 13, Fibrous infraorbital arch; 14, Sternothyroid muscle; 15, Thyrohyoid; 16, Sternohyoid; 17, Thyroid cartilage; 18, Thyroid gland; 19, Mylohyoid; 20, Masseter; 21, Temporal; 22, Rhomboideus capitis; 23, Semispinalis capitis; 24, Splenius; 25, Spinalis dorsi; 26, Longissimus dorsi; 27, Transversarius superior; 28, Obliquus superior; 29, Rectus lateralis; 30, Levator anguli scapulæ; 31, Scalenus posticus; 32, Scalenus medius; 33, Sternomastoid and mastohumeral; 34, Sternomastoid origin; 35, Sternum; 36, Pectoralis minor; 37, Rectus abdominis; 38, Facial nerve; 39, Glossopharyngeal nerve; 40, Hypoglossal; 41, First cervical; 42, Second cervical; 43, Cord composed of third and fourth cervical; 44, Cord composed of fifth and sixth cervical; 45, Lesser brachial trunk; 46, Superficial cord of seventh and eighth cervical; 47, Nerve to serratus anticus; 48, Deep cord of seventh and eighth cervical; 49, Vagus.

caudal fasciculi arising from the premaxilla pass sagittally rostrad to be directly inserted into the recurved extremity of the blow-hole; the remainder converge to an aponeurosis which attaches to the extremity and rostral lip of the orifice. The aponeurosis is oval, covering the dorsum of the spiracular sac, and can be split into two layers in the greater part of its

¹ The deep portions of these muscles arising from the concavity of the face are intimately associated with the spiracular sacs; it is planned to report upon them in a subsequent paper dealing with the respiratory passages.

extent. Rostrad, however, where it receives the retractor muscle and the slip from the margin of the antorbital notch, the layers are fused inseparably.

The muscle of the left side has the same origin except that none of its bundles come from the premaxilla, which terminates on this side at the level of the nostril. Its deeper layer is greatly thickened and the muscle, contrary to that of the right side, attains its greatest bulk caudad. The less projection of the spiracular sac on the left affords space for the increase of the muscle. It inserts into the extremity of the blow-hole and the lateral part of its rostral lip directly; the aponeurosis is much reduced and, attached to the mid-region of the lip, involves only the more rostral fasciculi. Here again the topography of the spiracular sacs may be the explanation.

These muscles obviously act as dilators of the blow-hole, drawing forward its rostral lip and fixing its extremities. The greater bulk of the right muscle rostrad and of the left caudad would determine their greatest traction in the line of obliquity of the blow-hole; and the greater thickness of the left muscle is noteworthy, not only as assigning it the major rôle in opening the blow-hole and in consequence of its obliquity acting more favorably than its antimere upon the rostral lip, but also as being, by reason of its greater strength, itself a possible factor in the sinistral displacement of the narial aperture. The form and position of this orifice, its asymmetry, obliquity, and recurved extremities are precisely such as might seem to result from the disposition of these muscles the differences in which, associated with the topography of the spiracular sacs, depend ultimately upon the displacement of the larynx and the enlargement of the left, the reduction and secondary extreme modification of the right narial passage.

The second muscle of the ental group has a transverse origin at the base of the rostrum extending from the septal cartilage across the premaxilla and maxilla to the lateral margin of the latter bone. Here it lies immediately in front of the dilator. The muscle ascends dorsad, nearly vertically on the right, with more obliquity on the left, to the aponeurosis of the dilator. It broadens towards its insertion and becomes mixed with much fibro-areolar tissue, which gives it a tough consistency and pale color, and distinguishes it sharply from the dilator.

The muscles of the lateral group are similarly infiltrated with fibro-areolar tissue and break up into complicated interlacements in the cheek and lip that rendered their complete analysis in this foetus impossible. The most superficial stratum corresponds to the supraorbital bundle of the mystacocete, and is apparently the sole representative of the occipito-frontalis. At least, we could find no fasciculi of this layer arising from occipital and certainly none inserted into the margins of the blow-hole

superficial to the dilator. The supraorbital bundle is of considerable size. It arises broadly from the lateral surface of frontal, extending upon its orbital plate but not reaching the margin, and also upon the lateral surface of the maxillary. Here it is imperfectly separate from the origin of other fasciculi of differing course and deeper position. The supraorbital muscle then forms a band on the lateral surface of the dilator and, crossing the retractor, breaks up in the fibro-areolar tissue of the snout. Its fasciculi are dispersed in a radiation from its origin, ascending superficial to the dilator, turning mesad in front of the retractor, and descending in the cheek towards the lip and angulus oris, here becoming inextricably blended with the deeper bundles mentioned above. They are, in general, superficial to the other muscles of the region and all terminate in the blubber layer.

A deeper muscle has an extensive origin from the lateral surface of the maxillary tuberosity and malar and from the antorbital process of the frontal. Its numerous fasciculi extend rostrad through the cheek to the upper lip, or are lost near the angle of the mouth, or turning ventrad break up in the dense fibrous blubber of the cheek and over the mandible. They are blended with the bundles of the supraorbital muscle and further interlaced with fasciculi coming from the zygomatic process of the squamosal and from the proximal extremity of the mandible.

The mandibular slip has a mixed tendinous and fleshy origin from the angle of the lower jaw. Passing rostrad, it expands under cover of the slip from squamosal and its superficial bundles are lost in the cheek; its deeper fasciculi ascend towards the malar and the maxilla, some of them gaining an insertion in the vicinity of the antorbital notch. While having the same direction as the masseter, they are distinguished from it by their position superficial to the facial nerve.

From the zygomatic process and the fibrous infraorbital margin arises a fan-shaped muscle of superficial position which radiates into the cheek.

The buccinator is represented by fasciculi on the oral surface of the cheek close to the mucous membrane which are attached to the mandible behind the teeth and to the ventral surface of the maxilla. Extensions from this stratum pass into both upper and lower lips. The whole system is intimately united and blended with the deeper fasciculi of malar and maxillary origin.

The dorsal surface of the rostrum in front of the retractor gives rise to a thick muscle, which, radiating towards the surface, is lost in the thick blubber of the snout.

The orbicularis palpebrarum is well developed. It has an origin at both the pre- and postorbital process, the former being especially large. We were unable to define the auricular muscles.

As a whole, the facial musculature is characterized by its great size and extent, but, with the exception of the dilator naris, none of its elements were clearly differentiated. At sites of bony attachment, it was possible to define elements which, in their further course, became inextricably interwoven with other fasciculi in the dense fibro-areolar tissue of the region. In places where the latter was scanty, the tissue on section had much the structure of tongue.

Muscles of mastication. The masseter, in contrast to conditions

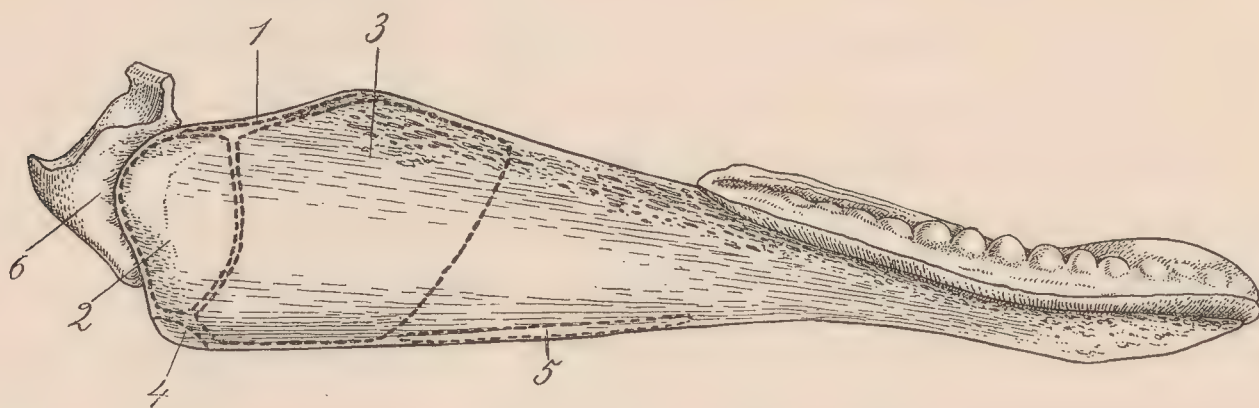


Fig. 9. Lateral surface of mandible; the rudiments of the teeth and surrounding gums are left in place. Half natural size.

1, Temporal muscle; 2, Masseter, superficial portion; 3, Masseter, deep portion; 4, Slip of facial muscle; 5, Hyomandibularis; 6, Temporo-maxillary fibro-cartilage.

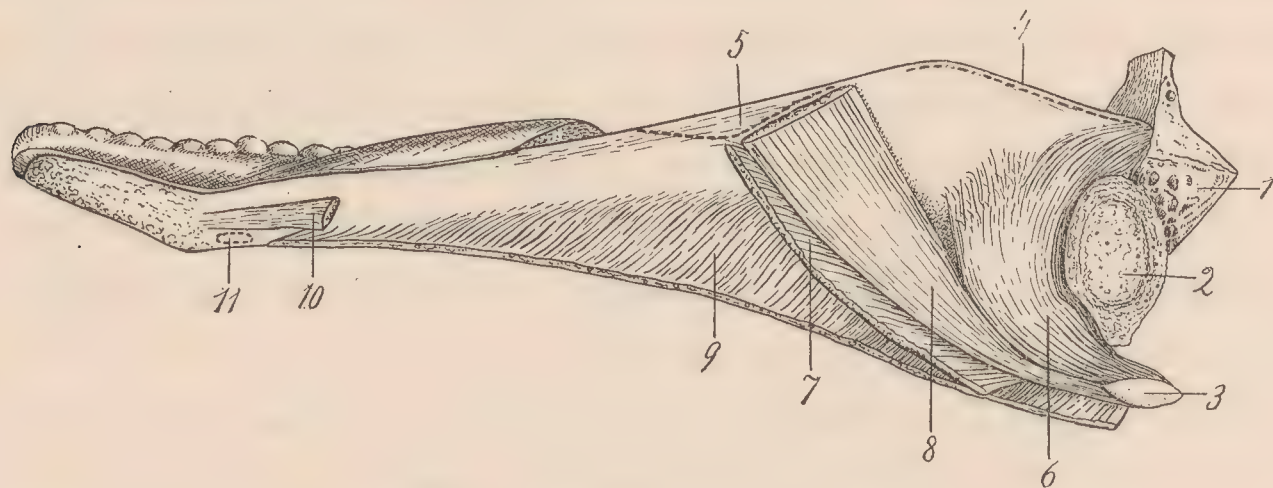


Fig. 10. Mesal view of mandible and attached muscles. Half natural size.

1, Temporo-maxillary fibro-cartilage; 2, Meckel's cartilage; 3, Stylo-mandibular ligament; 4, Temporal muscle; 5, Buccinator; 6, External pterygoid; 7, Internal pterygoid; 8, The same, deep portion; 9, Mylohyoid; 10, Genioglossus; 11, Geniohyoid.

described in *Phocæna* and *Globicephalus*, is a large muscle, divided also into two portions. Our dissection of the superficial portion was imperfect, but this much was ascertained. It arose from the rostral border and tip of the malar and from the fibrous infraorbital arcade. At the origin we could not disentangle it from the massive facial muscle of the region, but very soon the great trunk of the facial nerve was interposed, and from that point to the insertion the muscle could be satisfactorily isolated, except at its rostral margin which could be located only approximately. The same

is true of the deep portion also. The great fibro-muscular interlacement of the cheek seems to involve both of them, together with overlying facial muscles and the deeper buccinator, in a mass that we failed to analyze. From the origin above described, the bundles of the pars superficialis expand to an extensive insertion upon the mandible occupying its whole proximal portion, except the angle which gives origin to a slip of facial innervation and an area near the dorsal margin occupied by the pars profunda. This also arises from the malar, extending upon its mesal surface. The belly expands fan-wise to its insertion. This is, in general, dorsal and rostral to the superficial portion. It includes the border between the condylar process and the superior angle and the dorsal border thence for about two-thirds the length of the pars papyracea, extending ventrad to the insertion of the deep portion and in front of it reaching the ventral margin of the bone for a short distance. The obliquity of the bundles in both portions is such that their contraction must protrude, as well as approximate, the mandible to the maxilla.

The temporal muscle is rather small, but thick. It arises from the whole of the temporal fossa and the ental surface of the zygomatic process. Additional fasciculi are derived from its covering aponeurosis. There is little convergence of its bundles. The insertion is into the dorsal border of the mandible from a little above the condyle to the superior angle (coronoid process) and into the adjacent mesial surface to a moderate degree.

The pterygoideus internus is essentially like that of *Phocæna*, as described by Stannius. The superficial layer arises from the margin of the pterygoid bone from its caudal extremity to the beginning of the infrapalatine process, here becoming thin and aponeurotic. At the pterygoid notch, the muscle is not interrupted but arises from a ligament which spans the notch. The bundles, directed caudad and laterad, form a thin narrow sheet which invests the air-sinus ventrally. The insertion is into an oblique line on the mandible and the fibrous tissue enclosing the deltoid foramen, from the rostral end of the temporal insertion to the angle of the jaw, and slightly into the strong ligament between the angle of the mandible and the styloid process. The deep portion is narrower and applied to the superficial close to its insertion. It arises from the infrapalatine process of the pterygoid. In the adult skull, the muscular impression extends upon the maxilla, but, in the foetus, we could not follow the tenuous sheet so far. The muscle descends obliquely, contracting to a narrow belly which inserts at the angle of the jaw and into the ligament extending thence to the styloid process.

The external pterygoid is greatly modified by the presence of the air-sinus and partially blended with the deep stratum of the internal. It arises from the mandibulo-styloid ligament and spreads out fan-wise as it ascends

upon the lateral wall of the air-sinus, here resting against the huge remnant of Meckel's cartilage. Arrived at its dorsal border, it is in part inserted into the fibrous wall of the sinus but a very considerable number of its caudal fasciculi pass laterad above Meckel's cartilage and converge to an insertion into the condylar process of the mandible and into the mesial aspect of the interarticular fibro-cartilage.

The suspension of the mandible is effected by means of a large pyramidal cartilage. The base of this is saddle-shaped and attached to the periosteum of the extremity and ental surface of the zygomatic process of the squamosal. The rostral border is applied in a similar way to the mandible from the condyle almost to the angle of the bone. Superficially, the cartilage is covered by a dense membrane which extends from the mandible to the tympano-mastoid and ventrally thickens to form the very strong stylo-mandibular ligament. The membrane serves as origin to the depressor mandibulæ and by its deep surface covers a mass of vascular or really cavernous tissue which surrounds Meckel's cartilage and fills the interval between the jaw and osseous bulla tympani. Against this tissue, the interarticular fibro-cartilage rests its deep surface. The joint is peculiar in the total absence of a cavity, a condition obtaining also in *Balænoptera*.¹ In this connection it may be noted that in other joints of this foetus, the occipito-atlantal and the scapulo-humeral, the surfaces of the articular cartilages were covered by a moderately thick layer of perichondrium continuous with the periosteum of the bones.

Suprahyoid muscles. The most superficial muscle of the intermandibular region is a broad, longitudinal sheet of fasciculi arising from the hyoid close to the insertion of the sterno-hyoid and continuing the direction of that muscle to the jaw and cheek. No bundles were found continuous between these muscles. Rostrad, the muscle divides into two layers: a deep layer inserts into the ventral margin of the mandible in its middle third; a superficial stratum is lost in the interlacement of the cheek. The most rostral fasciculi of this layer are prolonged in a well defined slip beyond the angulus oris to the upper lip. The muscle here described rests upon the mylohyoid and is innervated by the mylohyoid branch of the fifth nerve as it lies between them. The muscle is, then, the hyomandibularis, often modified in other forms into the anterior belly of the digastric. Le Danois seems to have mistaken this muscle for the mylohyoid, which he describes and figures with sagittally directed bundles.

The mylohyoid in this specimen has the usual transverse orientation and

¹ Beauregard, H. Étude de l'articulation temporo-maxillaire chez les Balænoptères. Jour. de l'Anat. et de la Physiol., An. 18, 1882.

is a strong and well developed muscle. It arises under cover of the hyomandibularis from the margin of the hyoid from its tip to the median line along which its origin is continued to the symphysis by a feebly developed

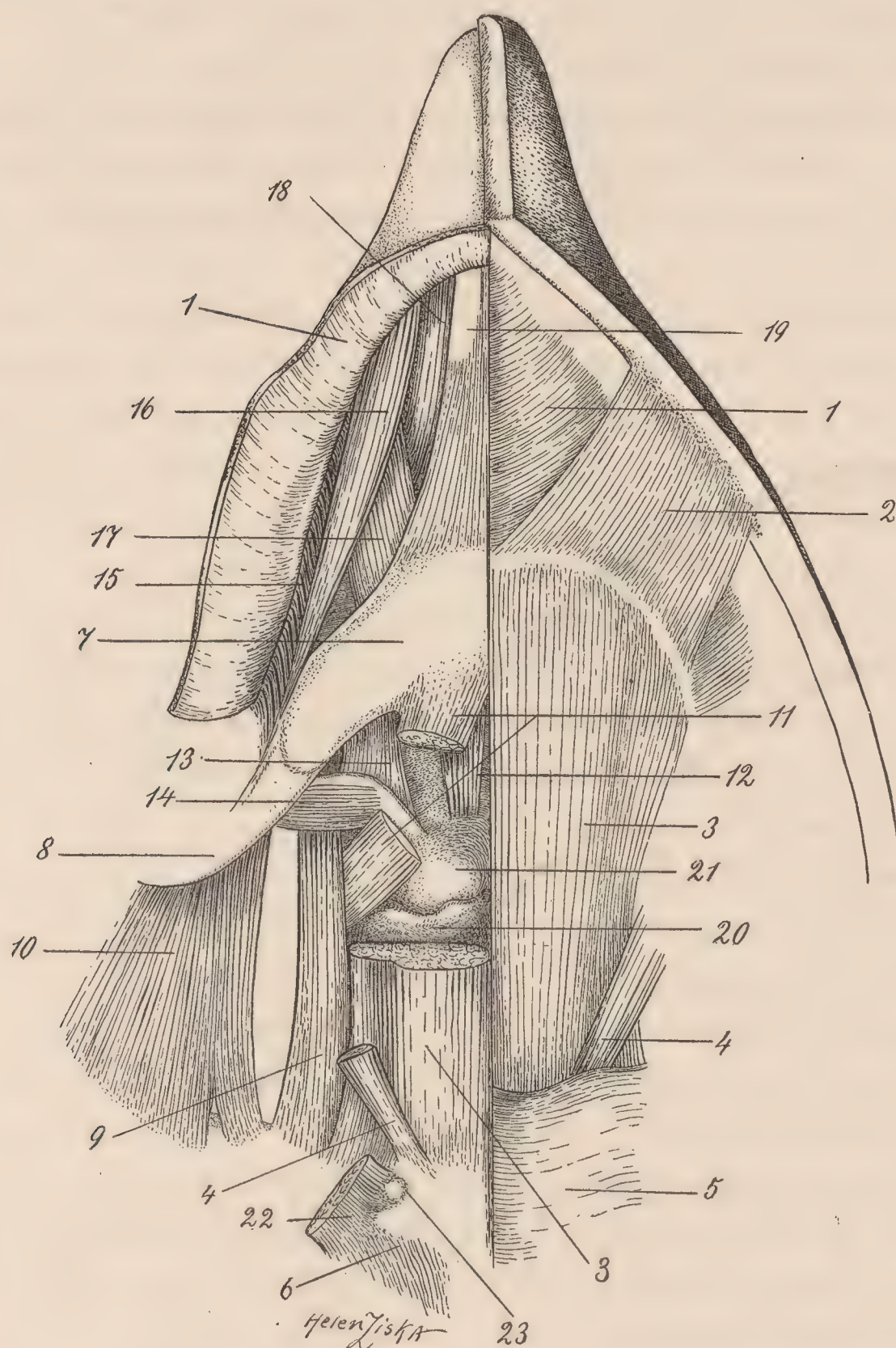


Fig. 11. Muscles of the intermandibular region and throat.

1, Mylohyoid; 2, Hyomandibularis; 3, Sternohyoid; 4, Sternomastoid; 5, Ectopectoral; 6, Rectus abdominis; 7, Hyoid; 8, Stylohyal; 9, Sternothyroid; 10, Scalenus medius; 11, Thyrohyoid; 12, Hyo-epiglotticus; 13, Pterygo-pharngaeus; 14, Inferior constrictor; 15, Internal pterygoid; 16, Styloglossus; 17, Hyoglossus; 18, Genioglossus; 19, Geniohyoid; 20, Thyroid gland; 21, Thyroid cartilage; 22, Entopectoral; 23, Episternal ossicle.

raphe. The fasciculi pass transversely to be inserted into the oral surface of the mandible along a line which ascends to the attachment of the buccinator and then descends to the angle of the jaw.

At the caudal margin of the mylohyoid and continuing its sheet is a

small flat muscle distinguishable from it only by its origin and its innervation. It arises from the hyomandibular ligament and the dense fibrous tissue stretching between the mandible and the tympano-mastoid. It is inserted into the tip of the hyoid continuously with the mylohyoid. Its nerve is a branch of the facial. The last fact serves to identify it as the depressor mandibulæ, the equivalent of the posterior belly of the digastric. In *Phocæna*, the homologue of this muscle, the occipito-hyoideus of Rapp and Stannius, has retained a more primitive position as regards its origin. In *Tursiops*, Chaîne¹ found no homologue of the posterior belly of the digastric.

The hyoglossus is a ribbon-shaped muscle of moderate size. It arises from the ventral surface of the ceratohyal and from the adjacent margin of the body and is directed obliquely laterad, dorsad, and rostrad to the side of the tongue, where it disappears under cover of the styloglossus. It is crossed superficially by the hypoglossal nerve, from which it receives a branch, and beneath it lie the plexiform lingual vessels.

The geniohyoid arises from the symphysis and the adjacent portion of the ventral margins of the mandibles, and is inserted into the mesal half of the margin of the hyoid between the mylohyoid and hypoglossus. It is a well-developed, triangular muscle, the lateral portion of which, near its origin, is tendinous.

The genioglossus has lost its attachment to the hyoid, as in *Phocæna* (according to Rapp and Stannius). It has a pointed origin from the symphysis dorsal to the geniohyoid. Its fasciculi radiate in the usual manner into the dorsum of the tongue from the tip caudad. Some of the most ventral bundles are continued dorsal to the hyoid to the oropharyngeal passage. These two muscles are innervated by the hypoglossal nerve.

The styloglossus arises from about the middle of the stylohyal and is directed rostrad, expanding to its insertion into the side of the tongue superficial to the hyoglossus. It is not rudimentary, as in *Phocæna* (according to Stannius), but is of good size.

The interval between the thyrohyal, the stylohyal, the ceratohyal, and body of the hyoid is filled by a muscle, the fasciculi of which run ventrad from the stylohyal expanding to occupy a large area on the dorsum of the thyrohyal and body from the tip of the former to near the median line. This is the ceratohyal or hyoideus latus. It is supplied by the glosso-pharyngeal nerve.

The stylopharyngeus is of moderate size, arising from the stylohyal

¹ Chaîne, J. Le digastrique (Abaisseur de la mandibule des mammifères). Jour. de l'Anat. et de la Physiol., 1914.

dorsal to the foregoing. From the mesal aspect of the cartilage its bundles run mesad and rostrad to the interval between the pterygo-pharyngeus and palato-pharyngeus, where it reaches the wall of the pharynx.

Infrahyoid muscles. The sterno-hyoid is a very large muscle. It arises from the rostral border of the sternum in nearly its whole breadth, and mesially its origin extends upon the venter of the manubrium between the origins of the ectopectoral and the sterno-mastoid. The belly of the latter muscle rests in a groove in the sterno-hyoid, partially separating the deeper fasciculi of lateral origin from those just mentioned as arising from the venter

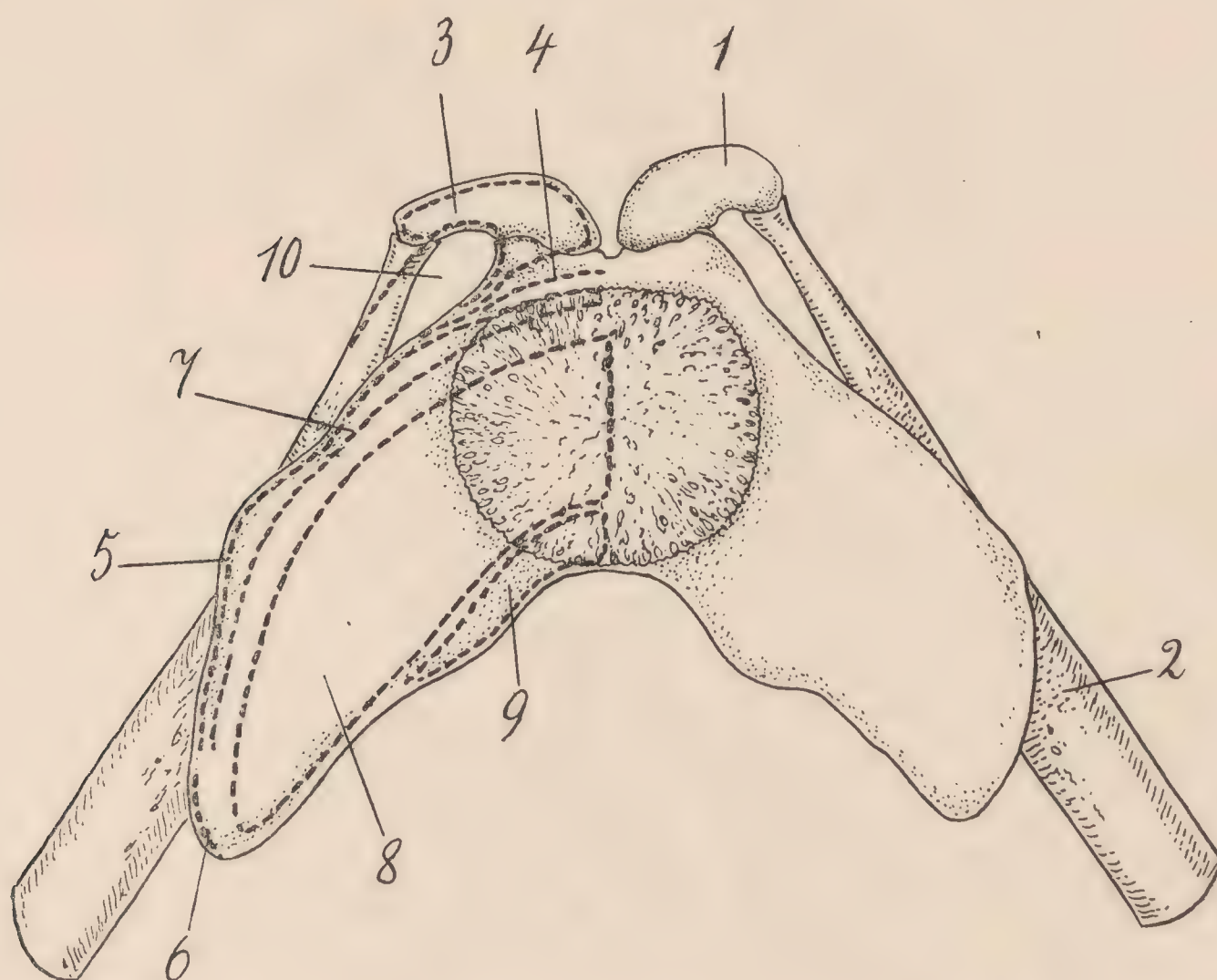


Fig. 12. Ventral view of hyoid, showing attachments of muscles. Half natural size.

1, Ceratohyal; 2, Stylohyal; 3, Hyoglossus; 4, Genioglossus; 5, Mylohyoid; 6, Depressor mandibulae; 7, Hyomandibularis; 8, Sternohyoid; 9, Thyrohyoid; 10, Hyoideus latus.

of the sternum. Higher in the neck, these bundles spread out and completely cover those coming from the sternal margin. The muscle, as a whole, broadens to its large insertion into the rostral margin and adjacent ventral surface of the hyoid, only a small area being left for the thyrohyoid mesad and caudad.

The sterno-hyoid is a much smaller muscle though of considerable development. It arises from the sternal margin, the cartilage of the first rib, and the capsule of the intervening joint. Mesially, it is in close contact with and partly overlapped by the sterno-hyoid. Its belly runs rostrad and slightly dorsad contracting somewhat to its insertion upon the thyroid cartilage between the thyrohyoid and the inferior constrictor of the pharynx.

The thyro-hyoid is a thin, flat muscle arising under cover of the foregoing from the thyroid cartilage, directed ventrad and rostrad, and widening and becoming thinner as it approaches its insertion into the venter of the body of the hyoid near the median line and caudal margin of that element.

There is no omo-hyoid on either side. Rapp and Stannius have previously recorded its absence in *Phocæna*.

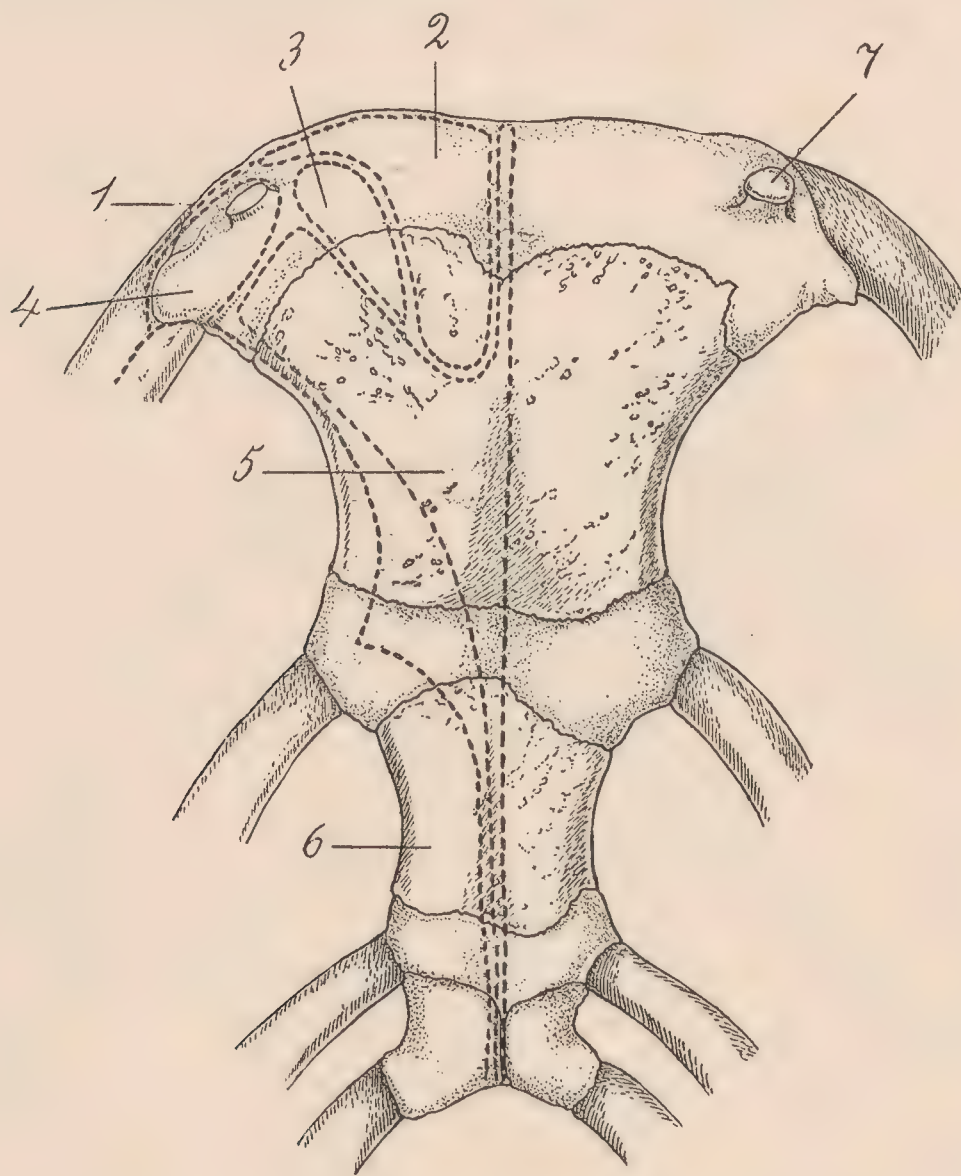


Fig. 13. Sternum, showing attachment of muscles. In the cartilaginous portion of the manubrium on each side is a small elevated facette which articulates with a nodule of cartilage (suprasternale) embedded in the origin of the entopectoral. Two-thirds natural size.

1, Sternothyroid; 2, Sternohyoid; 3, Sternomastoid; 4, Entopectoral; 5, Ectopectoral; 6, Rectus abdominis; 7, Suprasternal cartilage.

Costal muscles. Levatores costarum are present from the first to the eleventh thoracic vertebra. That of the first rib could not be distinguished from the mass of the scalenus posticus. They are best developed and most distinct from the external intercostal in the upper thorax; caudad they are reduced to a few fasciculi from the tip of the transverse process to the mesal margin of the intercostal. All are of the short variety, spreading out fan-like from the transverse process to the rostral margin of the next following rib. Their mesal fasciculi are sagittal and in many cases largely fibrous; their lateral ones have the inclination of the external intercostal.

The intercostals are well developed, especially the external. Its fasciculi are markedly oblique caudad and ventrad. Its fleshy bundles, as usual, are shorter than the distance between the ribs and are lengthened by tendons. These are associated with the insertion near the angles of the ribs, with the origin farther ventrad, though on the deep surface of the sheet there are fasciculi which are fleshy throughout. The muscles extend from the levatores costarum to the extremities of the ribs but are lacking upon the cartilages. The internal intercostal has an opposite inclination but is less oblique. In the ventral half of the rib, it is aponeurotic at its origin; the whole insertion and the dorsal part of the origin are fleshy. These muscles extend from the angles of the ribs to the sternum, connecting the cartilages as well as the bones. No interval was found segregating the intercartilaginous portions to form, as in *Phocæna*, the mm. ossium sterno-costalium of Stannius, and there seemed to be no lamination of the intercostal, such as recent students of human anatomy describe — the intercostalis intermedium of Eisler.

The sterno-costalis, described by Stannius in *Phocæna*, we failed to find.

The scalenus anticus is absent, the subclavian artery crossing the first rib entirely ventral to the muscles of this group. The scalenus medius is very large. It arises from the caudal portion and ental surface of the otocranial flange of the basi-occipital and, passing caudad through the neck, is inserted into the margin and ectal surface of the first rib from its extremity dorsad to the insertion of the scalenus posticus. The scalenus posticus though much smaller is yet of good development. It arises from the transverse process of the atlas and the succeeding cervical vertebræ and expands towards its insertion into the ectal surface and border of the first rib in the vicinity of the angle. Of these two muscles, the medius is by far the larger and, the origin being displaced ventrad by the projection of the otocranial flange, its course is almost sagittal. It must, therefore, act with maximum efficiency as an elevator of the first rib. In consequence of the displacement of the origin of the medius, the two muscles are widely separated except at their insertions and a large interval is left in which emerge branches of the cervical plexus; others make their way through the substance of the medius.

The diaphragm. The highest point of the diaphragm corresponds, as nearly as can be ascertained in the relaxed condition of the viscera, to the space between the third and fourth ribs. From this point it descends slightly ventrad to the lower end of the sternum, the deep sheath of the rectus, and the cartilages of the fifth ribs. Dorsally the slope is steep and prolonged to the sheath of the hypaxial muscle, here extending as far caudad as the third lumbar vertebra.

As in odontocetes in general (O. Müller¹), the centrum tendineum is greatly reduced. In this specimen, a small triangular area of the aponeurosis persists on the caudal aspect of the foramen for the postcava. Elsewhere there are scattered fibrous bands on the abdominal surface along the junction of the sternocostal portion with the lumbar. The crura also are largely fibrous and, after joining ventrad of the aortic orifice, are prolonged by a strand of connective tissue to the oesophageal foramen. Caudad, the crura expand into a fibrous sheet which stretches across the hypaxial muscle to the tip of the last rib and is intimately united to the

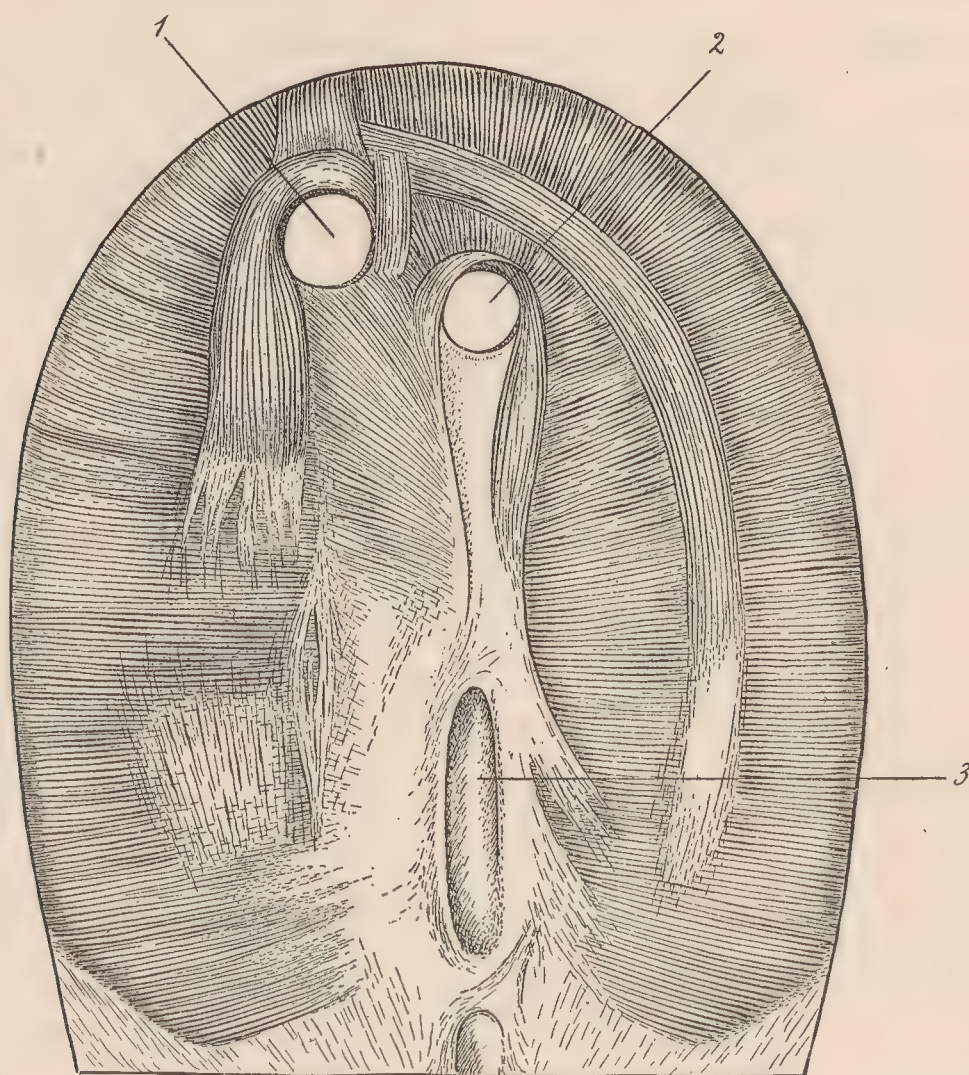


Fig. 14. Abdominal surface of diaphragm.

1, Foramen for postcava; 2, Foramen for oesophagus; 3, Aortic aperture.

sheath of the muscle and the transversalis fascia. From this no muscular bundles are derived. It serves simply to fill the interval caudad between the last costal digitation and the fasciculi arising from the crus mediale. While the crus laterale thus fails of reaching the ligamentum arcuatum, it is not entirely lacking, if we are right in taking as its equivalent the superficial longitudinal bundles which, following the line of junction of the pars sternocostalis with the crura medialis, converge to the foramen venæ cavæ.

¹ Müller, O. Untersuchungen über die Veränderungen welche die Respirationsorgane der Säugetiere durch Anpassung an das Leben in Wasser erlitten haben. *Jenaische Zeitsch. f. Naturwiss.* XXXII, 1898.

The sternocostal portion forms a continuous sheet of a horseshoe shape, its bundles converging to meet the ental region derived from the crura. The pars sternalis arises from the caudal piece of the sternum and from the sheath of the rectus; at the sides it is perfectly continuous with the costal portion. This arises from the ends of the ribs and their cartilages, from the fourth to the twelfth, interdigitating with the transversalis. The lowermost fasciculi insert into the fibrous expansion of the medial crus above mentioned. The remainder meet the deeper bundles of the crus along a linear junction, which is U-shaped, the arms converging to the foramen venæ cavæ. In much of its course this is concealed by longitudinal fasciculi arising on each side from superficial, tendinous bands, lateral to the crus mediale and converging in a wide arch to the venous foramen where they are interwoven with bundles of the other portions of the muscle.

The crura medialis arise fibrous from the bodies of the first three lumbar vertebræ. Near their origin, they are associated with lateral expansions which are continued into the arcuate ligaments and, higher up, receive the lowest fasciculi of costal origin. The two crura unite ventral to the aorta in an arch, from which a fibrous raphe is prolonged to the œsophageal orifice. To this raphe, on its thoracic surface, is attached the strong fold that in the lower thorax bridges between the aorta and œsophagus. The muscle originating from the crura and raphe is partially divided into a deep and a superficial stratum. The superficial stratum forms a loop about the œsophageal foramen. On the left side, this is sharply defined against the deeper fibers, but on the right, in the interval between the œsophageal and venous foramina, the two layers merge, a small muscular ridge immediately adjacent to the former orifice alone remaining independent and continuing caudal beside the raphe reaches the point of union of the two crura. The deep layer is composed of bundles of a transverse to latero-rostral direction, which pass from the upper parts of the crura and their raphe to meet the sternocostal portion in a U-shaped line.

Abdominal muscles. The obliquus externus is a thin and rather narrow sheet of muscle upon the side of the thorax and abdomen. It arises by a somewhat irregular series of slips from all the ribs and, caudal to the twelfth, from an aponeurosis covering the hyaxial muscles and attached by means of the lateral intermuscular septum to the transverse processes of the lumbar vertebræ. The first slip is the largest and arises from the caudal margin of the first rib close to its cartilage. It is directed obliquely caudad and ventrad, skirting the origin of the first slip of the serratus anticus. The second slip arises from the caudal margin of the second rib and passes between the slips of the serratus. The third slip and all the more caudal ones are attached not only to the margins but to the lateral surfaces as well

of their respective ribs, immediately ventral to the insertions of the transversarius superior. The line of this interdigitation ascends caudad as the transversarius narrows. The remainder of the muscle arising from the lumbar aponeurosis is very thin. Its origin ceases about midway between the preputial orifice and the vent. All of the costal slips have an admixture of aponeurotic fibers at their origin. The third digitation on both sides is peculiar in the expansion of the dorsal part of its origin by a tendinous slip to the caudad margin of the second rib. A similar extension is present on the part of the second digitation of the right side, which falls short of the first rib and is attached to the fascia of the first intercostal space. The several slips unite to form a muscular sheet of parallel bundles, which continue to the edge of the rectus where they abruptly become aponeurotic and invest that muscle with a thin but very strong covering as far as its median border. Rostrad to the preputial orifice, they interlace with their antimere. Caudad, where the recti are partially separated by the penis, they are less distinct and are lost upon the surface of the muscle or merged in the thick connective tissue that ensheaths the penis. The relation of the external oblique to the margin of the rectus requires some further comment. While the superficial bundles are continued as is usual into a superficial aponeurosis of the rectus sheath, deep bundles remaining fleshy are interwoven with the lateral fasciculi of the rectus itself and, in the caudal half of the muscle, also with bundles of the obliquus internus, which pass between them to gain the superficial aponeurosis of that muscle or, on the other hand, take a deeper course into the lateral portion of the rectus.

The internal oblique extends farther caudad than the external, arising from the lumbar aponeurosis from a point opposite the anus; rostrad, the origin extends to the last rib. The fasciculi form a thin sheet of very oblique direction. Those of most caudal origin are parallel to the aponeurosis of insertion of the rectus and as they are followed rostrad add themselves to the lateral portion of that muscle. Those of intermediate origin divide at the margin of the rectus and, becoming aponeurotic, form superficial and deep laminae which participate in the usual way in the formation of the sheath. Those of the superficial lamella, however, are interlaced with fasciculi of the external oblique in the manner described above. Between these superficial and deep layers there are additional fleshy bundles which become incorporated into the lateral portion of the rectus. The most rostral portion of the obliquus internus forms a broad layer covering the ventral ends of the free ribs and their cartilages, from the twelfth to the fourth inclusive. The insertions are into the caudal margins of the ribs and into their lateral surfaces, which they occupy in their whole breadth ventral to the obliquus externus as far as the extremities of the cartilages. In the reflection of this

portion of the muscle, many deep fasciculi were found which, arising from the rostral margin of one rib, inserted upon the caudal border of the next in front.

The transversalis is well developed and common to both thorax and abdomen. It arises from the hypaxial aponeurosis, extending not quite as far caudad as the internal oblique. It further arises from the ental surface of the ribs and costal cartilages, from the twelfth to the first inclusive. It forms a thick sheet coarsely fasciculate and of transverse direction, and is inserted into the sternum, the linea alba, and its caudal expansion. The transversalis thoracis is perfectly continuous with the muscle of the abdomen. It comprises the slips from the first four ribs which insert upon the dorsum of the sternum. These are well developed, but I could not separate them into two layers. Their insertion by mixed fleshy and tendinous bundles occupies the whole breadth of the sternum from the lower half of the manubrium to its extremity. The muscle is, in its whole abdominal extent, separable into two lamellæ separated by a distinct, though thin, fascia and further distinguished by a difference in the direction of their fasciculi, those of the deeper stratum being inclined a little caudad. The superficial lamella shows distinct digitations in its thoracic portion; these become tendinous ventrad and are inserted into the sheath of the rectus a little farther from the midline than the deeper stratum. The aponeurotic termination and lateral insertion characterizes the whole lamella; caudad also, where it takes origin from the hypaxial aponeurosis, it is sometimes divided into slips. The deeper layer forms a continuous sheet and is of greater thickness than the superficial. Its costal portion is fleshy to its insertion into the linea alba. Caudad, where the linea alba expands, it also becomes aponeurotic and fuses with the deep surface of the rectus sheath.

Such a reduplication of the transversalis, although occurring in reptiles,¹ is not often recorded in mammals and is not mentioned by Leche.² A partial reduplication, however, occurs in man,³ and frequently in the dog⁴; and, therefore, the condition here recorded ought not to be taken as suggestive of any peculiarly sauropsid affinities on the part of cetaceans, among which, in general, it seems not to occur.

The rectus abdominis is massive. It arises from the lateral margin of the manubrium, from the ventral surface of the following sternobræ, and from the cartilages of the first four ribs. Of the costal digitations, the first

¹ Maurer, L. Die ventrale Rumpfmuskulatur einiger Reptilien.

² Leche, W. Die Säugethiere in Braun's Thier-Reich. Bd. VI, Th. I. Leipzig, 1874-1900.

³ Eisler, P. Die Muskeln des Stammes. Jena, 1912.

⁴ Personal communication of Dr. A. J. Brown.

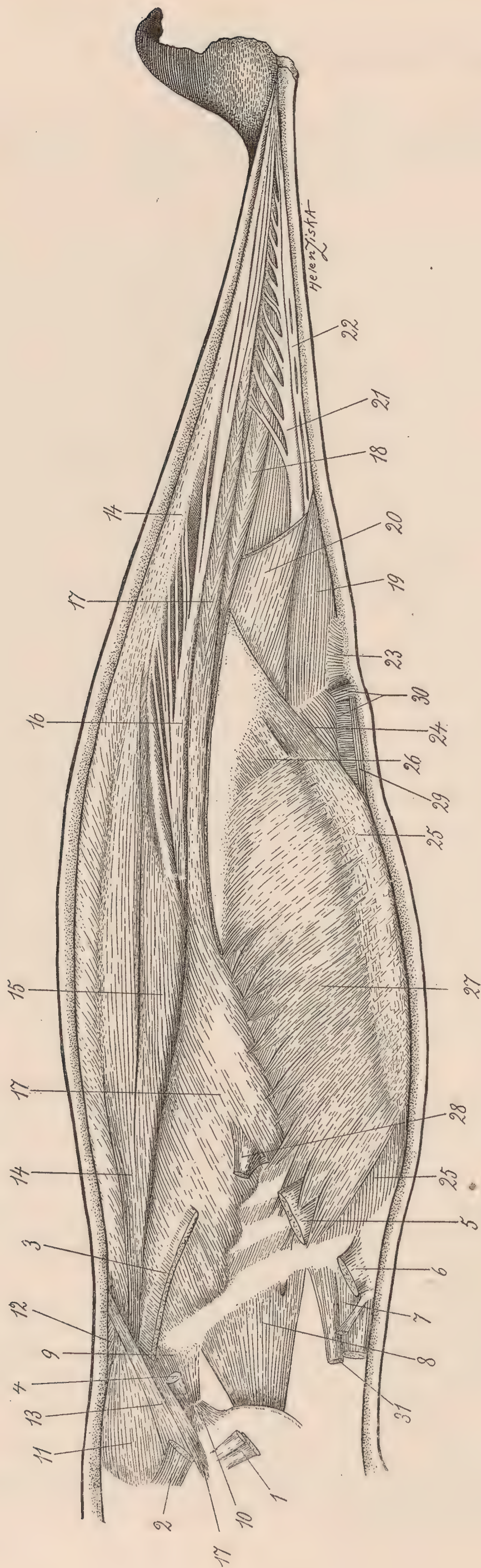


Fig. 15. Muscles of trunk; superficial dissection. The longissimus is partially turned up at the margin to show tendons to the iliocostalis.

1, Sternomastoid and mastohumeral; 2, Rhomboideus capitis; 3, Rhomboideus vertebralis; 4, Levator anguli scapulæ; 5, Serratus anticus; 6, Pectoralis minor; 7, Sternohyoid; 8, Scalenus medius; 9, Scalenus posticus; 10, Rectus capitis lateralis; 11, Semispinalis capitis; 12, Spinalis dorsi; 13, Splenius; 14, Longissimus; 15, Iliocostalis thoracis; 16, Iliocostalis lumborum; 17, Transversarius superior; 18, Transversarius inferior; 19, Ischio-caudalis; 20, Hypaxial muscle, superficial portion; 21, The same, lateral portion; 22, The same, ventral portion; 23, Levator ani; 24, Ischio-cavernosus; 25, Rectus abdominis; 26, Obliquus internus; 27, Obliquus externus; 28, Latissimus dorsi; 29, Retractor penis; 30, Bulbo-cavernosus; 31, Sterno-thyroid.

is the largest. The others join the deep surface of the muscle and are not seen until it is reflected. The belly extends sagittally the whole length of the abdomen and is devoid of tendinous inscriptions. Arrived at the pelvic ligament to which it has a small tendinous attachment, it expands into an aponeurosis which, merged with that covering the hypaxial muscles, is attached to the transverse processes of the lumbo-caudal vertebræ. Between the pelvic tendon and this aponeurosis is an interval of areolar tissue through which the vessels and nerves pass to the venter of the pedicle. The muscles of the two sides are in apposition as far as the umbilicus and united by a linea alba. To accommodate the large penis, they then diverge and their mesal borders are united by a very strong aponeurosis, which is equivalent to an expanded linea alba. This extends between the muscles to the pelvic region and there, laterally, is continuous with the deep tendon of the rectus. The fibrous interval is reinforced entally by the united aponeuroses of the internal oblique and transversalis, which here become very thick and strong. This area serves as an attachment for many of the bundles of the rectus, and, in consequence, the muscle rapidly diminishes in size, its continuation into the hypaxial aponeurosis representing only about one-third of its cross-section. The sheath of the rectus has the usual composition: its ventral layer formed of external oblique and the ventral aponeurosis of the internal oblique; its dorsal, of the dorsal lamina of the latter muscle and the transversalis. Everywhere the rectus adheres closely to the ventral sheath, which is composed of intersecting fibrous bands corresponding to the direction of the two component muscles. Rostrad of the first digitation of the external oblique the sheath is tenuous. Entally the belly of the rectus is easily separable from its sheath, especially the transversalis layer as far as the preputial orifice. Thence caudad it gradually becomes broadly adherent as its fasciculi terminate in the manner indicated above, and gradually the transversalis layer becomes more broadly and intimately adherent. The fixation of the rectus and the integrity of the abdominal wall is further secured by the connections of the margins with the interlacing fasciculi of the oblique. As the rectus turns laterad to its superficial insertion, its fasciculi are parallel and lie in the same sheet with those of the internal oblique. Indeed, the two muscles are not wholly separable. Farther rostrad, where the oblique splits to enclose the rectus, the cleft occurs in the flesh of the muscle (as in *Phocæna*, according to Stannius), and intermediate bundles, failing to reach either layer of the sheath, add themselves to the margin of the rectus.

Pelvic muscles. Benham, after careful search, was able to find no pelvis in a male *Kogia*. Le Danois does not mention it; and we, on dissection, are also unable to ascertain its presence. Its place is occupied by a very

dense lamella of white fibrous tissue which unites the ischiocavernosus to the bulbocavernosus. Caudad, this is continuous with the strong aponeurosis on the dorsum and the venter of the ischiocaudalis. As the former receives the deep tendon of the rectus abdominis and the latter gives attachment to the levator ani and retractor penis, the musculature of this region is as well secured as it could be by the presence of a rudimentary pelvis.

The ischiocaudalis is of moderate size. Its fasciculi arise mainly from its dorsal aponeurosis, which serves as an intermuscular septum between it and the hypaxial muscle and mesally joins its fellow of the opposite side. Bundles are also derived from the caudal end of the pelvic raphe between the ischio- and bulbocavernosus. The fasciculi pursue a sagittal course with a slight mesal inclination and are inserted into the sides of the first six chevron-bones, the fibrous tissue between them and, more ventrally, into the narrow but strong intermuscular septum between the ischiocaudales of the two sides.

The levator ani is well developed and of considerable thickness. It takes origin from the ventral fascia of the ischiocaudalis. Its fasciculi converge in a simple sheet towards the anal orifice, where they are blended with the wall of the anal canal, the bundles of the sphincter, and the panniculus.

The muscles of the penis have been described and figured by Benham and by Le Danois, and conditions in this foetus are in substantial agreement with their findings. The bulbocavernosus arises from the septum between it and the ischiocavernosus and, in front of that, form the sheath of the corpus cavernosum. It unites with its fellow below the corpus spongiosum in a narrow raphe. A loop of its caudal fasciculi passes ventral to the retractor to unite in a similar way with its antimere. This loop, which is narrow, rests against the levator ani. The retractor arises from the fibrous plane interposed between the levator ani and ischiocaudalis, which gives passage to the urethra and corresponds in a general way to the triangular ligament. The retractores then pass through the loop of the caudal bundles of the bulbocavernosus and pass side by side ventral to the rest of the bulb and corpus spongiosum to be inserted into the tunica propria at the level of the preputial sheath. The ischiocavernosi are well developed. They arise from the ventral aponeurosis of the ischiocaudalis and farther rostrad from the sheath of the hypaxial muscle. The fasciculi, which are nearly parallel, pass ventrad and rostrad to the septum between the ischio- and bulbocavernosus and also into the sheath of the corpus spongiosum.

Dorsal musculature. It is convenient for descriptive purposes to follow as closely as conditions permit the procedure of human anatomists in the classification and terminology of this very complex region. I have, there-

fore, made the magnificent study of Eisler¹ the basis of the following memoranda in these respects and have indicated where his usage departs from that of Stannius — with whose account of *Phocæna* the arrangement of *Kogia* conforms closely, especially when the variability of this region is taken into account. Leaving aside the transversarii which attain a peculiar development in Cetacea, the deep muscles of the back are divided into two layers: the first comprises the serrati postici; the second is subdivided into a lateral tract, a mesal tract, and the suboccipital muscles. The lateral tract includes the splenius, sacrolumbalis, and dorsal intertransversarii. The mesal tract is made up by the spinales, transverso-spinales (semi-spinales, multifidus, submultifidus), and the interspinales.

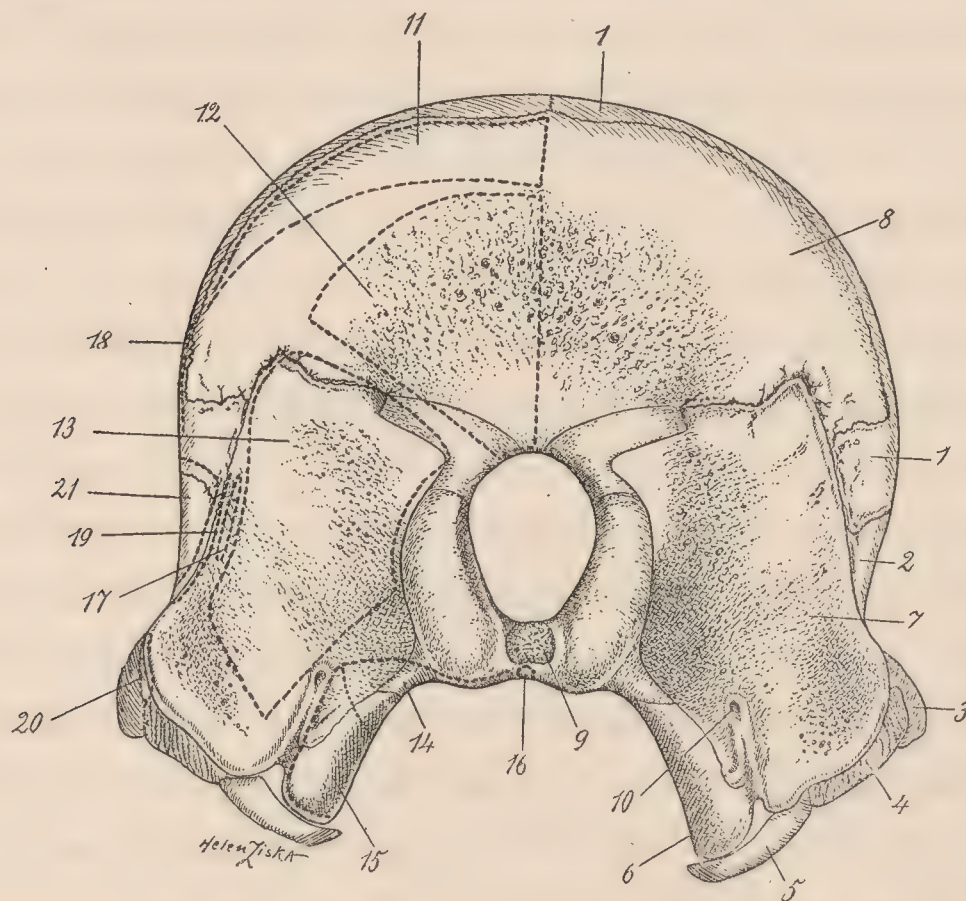


Fig. 16. Norma occipitalis, showing attachments of muscles. Two-thirds natural size.

1, Parietal; 2, Squamosal; 3, Zygoma; 4, Tympano-mastoid; 5, Stylohyal; 6, Otocranial flange; 7, Exoccipital; 8, Supraoccipital; 9, Caudal ossification center of basi-occipital; 10, Hypoglossal canal; 11, Semispinalis capitis; 12, Rectus posticus; 13, Rectus lateralis; 14, Rectus anticus; 15, Scalenus medius; 16, Longus colli; 17, Obliquus superior; 18, Rhomboideus capitis; 19, Splenius, longissimus, and transversarius; 20, Sternomastoid and mastohumeral; 21, Temporal.

These muscles, throughout pedicle and trunk, are segregated by a strong aponeurosis, a dorsal and a lateral septum. The dorsal septum extends between the spines; the lateral is attached to the transverse processes separating the dorsal muscles from the transversarius superior; the aponeurosis is attached to the tips of the spines and to the intermuscular septa, thus completing the compartment by a superficial investment. In the neck these fibrous structures, the dorsal septum excepted, become thinner and the lateral septum disappears altogether permitting a union between the

¹ Eisler, P. Die Muskeln des Stammes. Jena, 1912.

lateral tract and the transversarius. The shortening of the neck and in particular the reduction of the spines of the cervical vertebræ are associated with a diminution of the insertions upon this segment of the spine. In the case of several of the superficial elements these insertions are absent and muscles are prolonged to the occiput (*transversarius superior*) which do not usually in mammals reach the skull.

The *serrati postici* are absent as in other odontocetes (Rapp, Stannius, Murie).

The *splenius* is a rather small flat muscle arising from the dorsal intermuscular septum by an aponeurosis intimately adherent to that of the *longissimus dorsi*. Becoming muscular as it passes the lateral septum, it runs obliquely ventrad and rostrad parallel to the superficial *rhomboideus vertebralis* and beneath the *rhomboideus capitis* to the lateral border of the exoccipital, contracting slightly to its insertion by mixed fleshy and tendinous fibers. It is innervated by a branch derived from dorsal rami of the upper cervical nerve. At its insertion it is fused with the *iliocostalis capitis* and *transversarius superior*.

The *sacrospinalis* is composed of a lateral portion or *iliocostalis* corresponding to the *caudalis superior* and *sacro-lumbalis* of Stannius and a mesial portion, the *longissimus*. Both of these elements extend from the tip of the tail to the occiput and nowhere can they be completely separated. They are most independent in the pedicle where they are connected only by tendons of origin. As regards the lateral portion, the *iliocostalis lumborum* (*caudalis superior*) is almost a separate muscle; the *iliocostalis thoracis* is directly continued into the *capitis*; there is no connection with the cervical vertebræ. The last is true also of the *longissimus*. In its thoracic course, the latter muscle is separated partially from the *iliocostalis* by a thin septum which is visible on the surface but difficult to follow in the deeper parts. In the neck, it disappears and, towards the occipital insertion the separation of the two muscles, is artificial.

The *iliocostalis lumborum* extends from the last caudal to the sixth lumbar vertebra. It arises from the last caudal vertebræ by a tendon interposed between that of the *transversarius superior* and that of the *longissimus dorsi*. This tendon is reinforced by accretions from the vertebral centra as far as the fifteenth from the end of the series. Here the tendon begins to give rise to fleshy fasciculi and is soon concealed in the belly, which increases in size to the eleventh or twelfth lumbar vertebra and then diminishes to its termination at the sixth. At this point, only its deeper bundles are continued into the *iliocostalis* of the thorax; on the surface, the two portions are separated by a septum. The belly is increased by a series of tendons, eight in number, which come from the *longissimus*,

run in synovial sheaths through the intermuscular septum, and, entering the belly of the iliocostalis, are the source of incremental muscular fasciculi. This arrangement seems to be general among the Cetacea. The more caudal tendons are superficial and increase in size to the fourth. Rostrad, they diminish in size and are more deeply placed. The superficial fasciculi of the belly are sagittally directed, with an inclination ventrad, and are inserted into the septum intervening between the iliocostalis and the transversarius superior. The deeper bundles have fleshy attachments into the bodies and transverse processes beginning at the nineteenth lumbo-caudal vertebra. The breadth of the insertion broadens rostrad, on the one hand extending to the tip of the transverse processes as the transversarius superior narrows, and on the other hand extending mesad beneath the longissimus and iliocostalis thoracis to the accessory processes. It thus comes to be overlain in its whole breadth by the iliocostalis thoracis and, at the surface of apposition, is broadly continuous with it, the intermuscular septum disappearing. The region of fusion is just rostrad of the reception of the eighth tendon from the longissimus and caudal by the length of four vertebræ from the pointed termination of the lumbar muscle on the surface.

The iliocostalis thoracis is far more intimately united to the longissimus than the foregoing portion of this tract. On the surface, a narrow septum can be followed from the level of the fourth lumbar vertebra to the neck, where it disappears allowing the prolongations of the iliocostalis and longissimus to reach the exoccipital in a common insertion. This septum can not be followed deeply into the muscle, except as scanty connective tissue about the entering branches of the segmental nerves, so that many bundles are continuous from the longissimus into the lateral tract. If these nerves are taken as marking the arbitrary line of division, the iliocostalis may be said to correspond to the transverse processes; the longissimus, to the neural arches and accessory processes; and, save where separated by the spinalis, to the spines of the vertebræ. Its bundles are derived from the continuation of the iliocostalis lumborum at its start and from the longissimus in its whole length, the more lateral of the obliquely inclined fasciculi passing over uninterruptedly into the lateral tract. The insertions are fleshy into the upper lumbar transverse processes and the intervening fascia, into the transverse processes of the thoracic vertebræ, and into the ribs as far laterad as their angles, where they abut upon those of the transversarius superior. In the neck, the iliocostalis has no bony attachments but is continuous between the transversarius and longissimus to insert upon the exoccipital under cover of the splenius.

The longissimus extends the whole length of the axis from the last caudal vertebra to the exoccipital. It occupies the region beside the spinous

process as far as the middle of the thorax. Here the spinalis dorsi becomes independent and preempts the juxtaspinous position, and the semi-spinalis capitis, expanding rostrad, displaces the longissimus far to the side. In the pedicle, the muscle is best delimited; elsewhere it is blended laterad with the iliocostalis and mesad with the spinalis, which is recognizable only as fasciculi of more sagittal course and inserting upon the spinous processes, except rostrad where a septum is developed between the two muscles. As far as the mid-thorax, the longissimus is covered by a very dense aponeurosis of origin in its mesal portion. This is composed of oblique fibrous bands running rostrad and laterad from the tips of the spinous processes and the dorsal septum. After covering the muscle for a breadth of about an inch, it dips into its depth and can be followed nearly, but not quite, through its thickness. In *Phocæna*, Stannius found this septum dividing the longissimus from the iliocostalis (sacrolumbalis), but here it was embedded in the substance of the longissimus and is distinctly median to, and at some distance from, the superficial septum which we have taken as marking the boundary between these muscles in so far as it can be defined in *Kogia*. Caudad only at the beginning of the pedicle, just as the aponeurosis ceases to cover the whole surface of the muscle can it be said to effect such a separation, for here the fasciculi arising from its lateral surface are continued into the iliocostalis and reach insertions upon the ribs and transverse processes. Farther rostrad, fasciculi of similar origin constitute a broad tract between the lateral septum and the aponeurosis and are inserted into the neural arches and accessory processes. Fasciculi arise from the median side of the septum also and form a thick column, covered superficially by the aponeurosis; this is, in the greater part of the trunk, inseparable from the spinalis dorsi, but in the upper thorax defines itself by the lateral inclination of the bundles, some of them joining the more lateral portion of the longissimus while others are continued into the semispinalis capitis. Nowhere is a clean dissection possible.

The origin of the longissimus is by a series of tendons from the dorsal parts of the rudimentary caudal vertebræ, from the vertebral spines, directly and by means of the extensive aponeurosis on its surface, and by a series of tendons from the accessory processes. A large tendon is formed in the region of the last fifteen vertebræ by the union of successive tendinous slips. This then gives rise to fleshy bundles and the belly of the muscle rapidly increases in size by the addition of fasciculi from the deep surface of the investing aponeurosis. When the small spinous processes appear towards the middle of the pedicle, a series of tendons arise from their summits and from them bundles are added to the deeper parts of the muscle, which here rises high above the vertebræ. As the spines increase in size their sides

give rise to fleshy fasciculi and the tendons are transferred to the accessory processes. As has been said, the aponeurosis of origin dips deeply into the belly and fasciculi are derived from both its sides. This septum is directed from the surface towards the accessory processes and immediately below it are the tendons attached to these processes. Each tendon divides, and one division passes lateral, the other mesal, to the septum, so that the muscular derivatives of each tendon pass to both portions of the longissimus. In the middle third of the thorax, where the spinalis dorsi becomes defined and the semispinalis a little farther rostrad, the mesal arms of the tendons pass to these muscles, the lateral ones to the longissimus, and, as the spinalis increases in bulk, it gradually displaces the longissimus from the transverse processes — at first from their bases, later from their whole surface — so that it gives up all of its attachment to them, save for the aponeurosis from their tips and even this ceases in the upper third of the thorax.

The fasciculi have a nearly sagittal direction, the majority with a slight lateral inclination; thus they come to have a very long course between origin and insertion. Very many of them, as has been said, pass over into the iliocostalis or are carried into the deeper parts of the semispinalis capitis. Others, from the middle of the pedicle rostrad, have a sagittal direction and, inserting into the spinous processes, are representative of the spinalis dorsi, which becomes separable without injury of fasciculi only in the upper thorax and neck. Others, intermediate in position, form a tract which reaches the exoccipital in common with the iliocostalis. Of this tract, some of the deeper bundles are inserted into the bases of the transverse processes and the accessory processes of the rostral thoracic vertebræ, the iliocostalis being displaced laterad, for the tract diminishes in size to very moderate dimensions as it approaches the neck.

The spinalis dorsi is of small size in the pedicle and lower thorax and is inextricable from the mass of the longissimus. It appears on the surface in the upper thorax and is of considerable breadth when the aponeurosis of the longissimus ceases. Rostrad, it tapers to its termination on the dorsal tubercle of the atlas. Its fasciculi are derived from the longissimus, of which it constitutes a median tract. In addition to those coming from the belly and aponeurosis of that muscle, increments are derived from the tendons attached to the accessory processes. When it has attained sufficient size to displace the longissimus, it arises from the sides of the spinous processes, first at their bases and then in nearly their whole extent. The insertions are into the spinous processes and the equivalent tubercles of the cervical vertebræ. Deeply, the spinalis is intimately joined to the multifidus.

The semispinalis capitis is a large muscle. The pointed extremity of its

belly appears at the level of the seventh thoracic vertebra between the longissimus and the spinalis dorsi. Thence it expands rapidly to its insertion into the crest of the supraoccipital, which it occupies from the median line nearly in its whole breadth extending laterad to the insertion of the longissimus and splenius. Its fasciculi are, many of them, continued into it from the longissimus, but in addition it arises extensively from the aponeurosis of that muscle and receives large slips from the spinous processes of the upper thoracic vertebræ. In the neck, it has no attachments and is entirely free from the rectus posticus, in this respect differing from the homologue in *Phocæna* (according to Stannius).

The multifidus is represented by a series of oblique bundles arising from accessory processes and inserting upon the sides of the spines. In their course these elements pass over several vertebræ. Superficially, they are blended with the spinalis dorsi; deeply, with the submultifidus. The system is well developed from the upper lumbar region to the atlas; in the cervical region, its superficial bundles have a sagittal course and pass uninterruptedly from the first thoracic vertebra to the atlas; in the pedicle, it gradually diminished and was lost.

The submultifidus has about the same extent. It is composed of shorter bundles passing from accessory processes to the caudal margins of the spines and neural arches. The interspinales are well developed, especially between the large spines of the thorax.

These deep dorsal muscles conform closely to the account of conditions in *Phocæna* by Stannius.

The rectus capitis posticus is not resolvable into major and minor, or, more correctly, the minor alone is present, for the origin is confined to the dorsal arch of the atlas and no bundles are prolonged into the belly from the epistrophæus. It is a broad thick sheet of muscle, sagittally directed from its wide origin and inserted into the supraoccipital from the median line transversely to the suture of the exoccipital immediately ventral to the attachment of the semispinalis capitis. From this muscle it is entirely discrete, differing in this respect from conditions in *Phocæna* (according to Stannius) and in *Balænoptera*. In *Globicephalus*, Murie records both major and minor but intimately woven together.

The obliquus capitis superior lies at the lateral margin of the foregoing. In common with the rectus capitis lateralis, it arises from the transverse process of the atlas. Its belly is sagittally directed and in its proximal portion the surface is aponeurotic. It is inserted into the exoccipital beside the rectus posticus and, like it, is covered by the semispinalis.

The rectus capitis lateralis is short and triangular. Arising in common with the obliquus, it expands to a wide insertion upon the exoccipital,

occupying the area between the condyle and the lateral margin and extending ventrad to the level of the hypoglossal canal.

These three short muscles are supplied by the suboccipital nerve.

The transversarius superior is the most laterally placed of the dorsal muscles, following the line of the transverse processes and the costal angles throughout the length of the vertebral column. Its mesal border is separated by a strong septum from the members of the erector spinæ group and through this septum emerge the dorsal divisions of the segmental nerves. Superficially, the muscle and its tendons of origin are covered by a very dense sheath which extends rostrad as far as the last rib, beyond which it becomes tenuous. Ventrally, the sheath is attached to the sides of the centra and, where they are present, to the tips of the transverse processes which separate it from the transversarius inferior; dorsally, the sheath joins the lateral intermuscular septum. The muscle is thus well circumscribed as far as the last rib. Its lumbo-sacral portion is narrow; caudad, it is flattened against the sides of the centra; but, when transverse processes put in their appearance, it narrows slightly and becomes thicker, though not markedly. In this segment of its course, it is applied to the tips of the transverse processes and does not encroach upon their dorsal surface extensively, differing here in degree only from *Phocæna* (according to Stannius), which otherwise it closely resembles. Beneath its sheath, this portion of the muscle is covered by strong aponeurotic bands arranged in a herring-bone pattern with the angles pointing rostrad. This extends as far as the vent, proximad of which the fleshy fasciculi come to the surface. These are nearly sagittal in direction with only the slightest inclination ventrad as they pass from their origin upon the transverse process to their insertion on the last rib and on the septum between the transversarius and the great hypaxial muscle. The costal portion expands into a broad sheet, covering the side of the thorax and interdigitating with the external oblique. Stannius distinguishes (for the purpose of description only for the two portions are inseparable) between a mesal portion associated with the angles of the ribs and the expanded sheet upon the thorax. The mesal part is thicker and is further characterized by its tendinous insertion into the angles and more mesial portions of the ribs, the fasciculi turning mesad under cover of the longissimus to reach these insertions. In the remainder of the muscle, the bundles are oblique ventrad and rostrad and, on the surface, present an uninterrupted course. There are no inscriptions. They appear as a continuation of the bundles of the lumbo-caudal segment, reinforced laterally by a series of digitations from the caudal margins and lateral surfaces of the ribs. The sheet attains its greatest breadth on the fourth rib and narrows by a series of steps to the first. From the first rib, the muscle is carried

rostrad by a thick rounded prolongation to the exoccipital, where it is inserted in close apposition to a slip of the longissimus. This cervical segment, which is not described by Stannius, arises from the angle of the first rib dorsal to the scalenus posticus. On the right side, it is separated from the thoracic portion by an inscription; but, on the left, this was lacking and the fasciculi of the thoracic segment continued into it. At first clearly separated from the longissimus by a prolongation of the intermuscular septum and by emerging dorsal divisions of cervical nerves, it is barely separable towards the occiput from the longissimus slip which inserts upon the exoccipital. Its relation to septum and nerves, however, seem to establish its homodynamity with the transversarius. It is entirely free; indeed, widely separated from the cervical transverse processes, a massive vascular plexus intervening.

Stannius describes the origin as beginning by a tendon from the last caudal vertebra reinforced by a series of tendinous slips from the next succeeding centra. Unfortunately this region dried during the process of dissection, and we could follow the main tendon only to the thirteenth from the last of the series. From the vertebra in front of this, the origin became fleshy and the tendon was quickly concealed by muscle bundles arising from it and from the sides of the centra, subsequently from the tips of the transverse processes, and to a small extent from the septum separating it from the dorsal muscles proper. Where it rests upon the hypaxial muscle it receives but scanty accretion of new bundles and these from the septum, and the extreme tips of the transverse processes. In the thorax the origins are extensive from the caudal margins and lateral surfaces of the ribs as far as the second. The first rib at its angle gives rise to the bulk of the cervical prolongation. The insertions begin at the twelfth rib and thence rostrad are into the caudal margins and lateral surfaces of the ribs from a point mesal to their angles for a variable distance laterad, the extent of the attachments increasing as far as the fourth rib and thence decreasing to the first. The cervical prolongation is inserted into the exoccipital in conjunction with the longissimus and the splenius.

The transversarius inferior extends over the last thirty lumbo-caudal vertebræ and is placed against the ventral halves of the centra and on the ventral aspect of the transverse processes; in other respects it resembles closely the corresponding portion of the transversarius superior. A large tendon arises from the ultimate caudal vertebræ and is reinforced by tendinous slips as far as the sixteenth from the end of the series. Thence to the twentieth the origin is by fleshy fasciculi. The surface of the belly for more than half its length is covered by V-shaped aponeurotic bands. From the deep surface of these, fleshy fasciculi are derived, those from the dorsal

arms passing obliquely to the more caudal transverse processes, those from the ventral pursuing a more nearly sagittal course to more rostral transverse processes. The insertion is by a series of slips into the tips of the transverse processes from their first appearance to that of the twenty-ninth or thirtieth vertebra from the tail. We could not find a continuity on the part of this muscle with the transversarius superior, such as Stannius describes, but otherwise it closely resembles his account of conditions in *Phocæna*. The ends of the origin are crossed by those of the great hypaxial muscle from which they are separated by very dense fibrous tissue. When the bellies appear they are separated by a strong septum, which is connected with the deep fascia ensheathing them on the surface. The septum, deeply, is attached to the chevron bones.

The intertransversarii are well developed flat muscles stretching between the transverse processes. They are separated from the transversarius superior by its very strong aponeurotic sheath. The fascial separation from the transversarius inferior and rostrad to the termination of that muscle from the hypaxial mass is less robust, but the muscles are everywhere perfectly distinct and there is no continuity of bundles. The small muscles are immediately ventral to the dorsal division of the segmental nerves from which they receive branches.

The hypaxial muscles. In the muscles of this system, in the neck *Kogia* differs materially from the known members of the Delphinidæ in the absence of the rectus capitis anticus major, a large muscle in both *Phocæna* and *Globicephalus*. The rectus capitis anticus minor is of good size, arising from the arch and transverse process of the atlas and inserting broadly into the exoccipital and basioccipital, extending from the attachment of the rectus capitis lateralis to the median line. The muscles of the two sides are separated by a triangle of connective tissue at their origin but converge to their insertions, where they are to a slight degree blended with the scalenus medius. In all respects, it is very similar to its homologue in *Phocæna*. The longus colli is represented by a moderately developed inferior oblique portion and a weak superior oblique, while the longitudinal bundles are apparently wanting. The inferior oblique portion arises from the centra of the first five thoracic vertebræ; occupying, with its antimere, the whole ventral surface of the spine so that the bellies are in contact save for an intermuscular septum. The fasciculi pass rostrad and laterad, and are inserted upon the venter of the mass of fused cervical vertebræ at about its middle, the insertion beginning at some distance from the midline and extending obliquely to the capitular process for the first rib. The superior oblique portion is weak. It arises from the venter of the cervical mass immediately rostrad of the foregoing insertion. Its bundles converge to join those of its

antimere in a small insertion into the basioccipital between the ventral ends of the condyles and into the anterior atlanto-occipital ligament.

The hypaxial muscle of the lumbar region and pedicle is of great size, extending from the lower ribs to the extremity of the tail. Rapp, who has given a careful description of the muscle in *Phocæna*, has designated it the psoas magnus, to which it corresponds partially but with the inclusion of other elements (Stannius). In *Kogia* the mass is incompletely separable into three parts as in *Balaenoptera*. Two sets of tendons appear caudad; one ventral, one lateral in position. The ventral tendons are continued into a belly deeply placed against the centra and the bases of the transverse processes. This is covered and concealed in the natural position of the parts by the belly arising from the lateral tendons. The two portions are separated by a very strong septum in the pedicle and in this septum are contained the two sets of tendons and their synovial sheaths. In the lumbar region, the septum defaults and the two bellies fuse into a common mass. Superficially a strong sheath invests the muscle. This, in its proximal two-thirds, is the source of muscular bundles which pass rostrad and dorsad to the tips of the transverse processes, so constituting a third portion of the hypaxial mass.

Rapp and Stannius have described the strong fibrous sheath. Laterally it is attached to the sides of the centra and forms an intermuscular septum between the hypaxial muscle and the transversarius inferior. Where the latter terminates, the sheath gains an attachment to the tips of the transverse processes. Ventrally the attachment is to the tip of the chevrons and farther rostrad to the centra of the vertebræ. It forms a septum between the hypaxial mass and the ischiocaudalis and, in the abdominal region, becomes blended with the strong transversalis fascia.

The superficial investing portion of the muscle requires but little additional description. It arises from the proximal chevron bones by means of the septum above described and, more rostrally, from the fusion area of the sheath with the transversalis fascia. The insertion is into the last rib and the transverse processes of the lumbar vertebræ as far caudad as the eleventh. Deeply, its bundles fuse with the next portion of the muscle.

This, the derivative of the lateral set of tendons, is independent as far rostrad as the eighth lumbar vertebra. The great tendon arises from the centra of the caudal vertebræ in their latero-ventral portion and is reinforced by a series of slips from the sides of the more proximal vertebræ. These cross the transversarius inferior superficially. Ventrally, another set of segmental tendons are derived from the septum attached to the chevron-bones. Thus is formed a great tendon which divides before enter-

ing the belly into seven subsidiary tendons. These run, as has been said, in synovial sheaths in the septum on the deep surface of the muscle and successively enter its ventral margin. The insertion takes place, in common with the deepest part of the hypaxial mass, into the last ribs and the transverse processes of the first eight lumbar vertebræ. Caudal to this point, the muscle is independent and its fasciculi insert fleshy into the ventral surfaces of the transverse processes of the ninth, tenth, and eleventh vertebræ. Beyond the last named, the transversarius inferior intervenes and separates the hypaxial mass from the processes; its fasciculi then insert into the septum between the two muscles as far caudad as the twentieth lumbo-caudal vertebra.

The deepest portion of the hypaxial mass originates by a tendon arising from the venter of the last centrum and receiving accessory slips from the succeeding vertebræ as far as the twenty-fifth lumbo-caudal vertebra. The belly begins at the nineteenth vertebra, arising from the most dorsal of the slips into which the tendon divides; this is followed by nine others, the more ventral having increasingly long courses in the synovial sheaths of the intramuscular septum. The most ventral tendon can be followed as far as the eighth lumbo-sacral vertebra before entering the belly. This has, in general, a bipenniform arrangement, its fasciculi diverging from an axial fibrous line along which the tendons enter and themselves give rise to diverging fasciculi, which at first are independent but soon merge in the general mass. Thus the belly is partially resolvable into a series of superimposed parts, those coming from the more ventral tendons having a more superficial and rostral position. From the eighth lumbo-caudal vertebra this portion is fused with the more superficial parts of the muscle. The insertions are into the sides of the centra of the lumbo-caudal vertebræ from the twentieth rostrad and into the bases of the transverse processes. The fused proximal portion of the mass inserts into the whole venter of the transverse processes and the centra, the muscles of the two sides approaching one another so that they are only separated by a narrow cleft in which are lodged the aorta and venæ cavæ. On reaching the thorax, the muscle inserts into the whole length of the last rib and its cartilage on its ental surface. Ventrally, a small component is continued to the eleventh rib beyond the extremity of the twelfth; and, dorsally, in the region of the angles a large portion extends to the tenth and eleventh ribs.

PERIPHERAL NERVES

The condition of the superficial parts of the head interferred seriously with the dissection of the nerves, and our account of them is accordingly incomplete. Especially was this the case with the orbital contents. Of the oculomotor and patheticus we have nothing to record.

The trochlearis leaves the cranial cavity by passing through the posterior and upper part of the sphenoidal fissure. Its course is rostrad and laterad, and it crosses dorsal to the eye muscles to enter the substance of the superior oblique.

The ophthalmic division of the fifth nerve leaves the skull through the sphenoidal foramen. It crosses the orbit lying in relation to the roof and turns dorsad through the notch in the orbital margin of the frontal bone. The nasal portion reënters the skull through the sphenoidal fissure, passes mesad lying in a groove in the frontal bone, and finally leaves the skull through a small foramen in the ethmoid to enter the nasal fossa.¹

The second division of the trigeminal nerve emerges from the brain-case through the sphenoidal fissure. Its course is rostrad, crossing ventral to the attachment of the eye muscles to reach the canal in the superior maxilla corresponding to the infra-orbital canal. Just before entering this a branch is given off which probably goes to the sphenopalatine ganglion. Traversing the main canal in the maxilla, the trunk appears on the dorsal surface of that bone and continues rostrad lying in a groove on the maxilla. Branches are given off to surrounding structures but could not definitely be traced. There is a small branch which unites with a ganglion-like formation. This small mass of nerve tissue lies on the dorsum of the rostrum between the antorbital notch and the infra-orbital canal and receives branches from both fifth and seventh nerves.

The third division of the trigeminal nerve leaves the skull through the foramen ovale. Its course is at first directly laterad. Nearing the mandible, it gives branches supplying the temporalis muscle. It then turns at right angles to its former course and proceeds rostrad, paralleling the upper border of the mandible and lying dorsal to the large and degenerate remnant of Mechel's cartilage. It soon divides into two portions. The main division passes rostrad, giving off branches to the pterygoid muscles and branches which turn rostrad and dorsad to cross the upper border of the mandible probably to supply the masseter. It also gives numerous branches

¹ Cf. Schulte, The Skull of *Kogia breviceps* Blainv. Bull. Amer. Mus. Nat. History, XXXVII, Art. XVII, Pl. XLII.

to the mucus membrane of the alveolingual region and continues as the lingual nerve into the tongue.

The other division, corresponding to the inferior dental, curves ventrad, giving off a branch which passes caudad to reach the region of the ear.

The mylohyoid branch is given off as the nerve enters the inferior dental foramen. This pierces the fat and connective tissue near the border of the mylohyoid and then passes forward, paralleling the lower border of the jaw and lying superficial to the muscle, which it supplies together with the overlying hyomandibularis.

The facial nerve leaves the cranial cavity through the jugulo-acoustic foramen in company with the auditory nerve. It lies rostral to the auditory

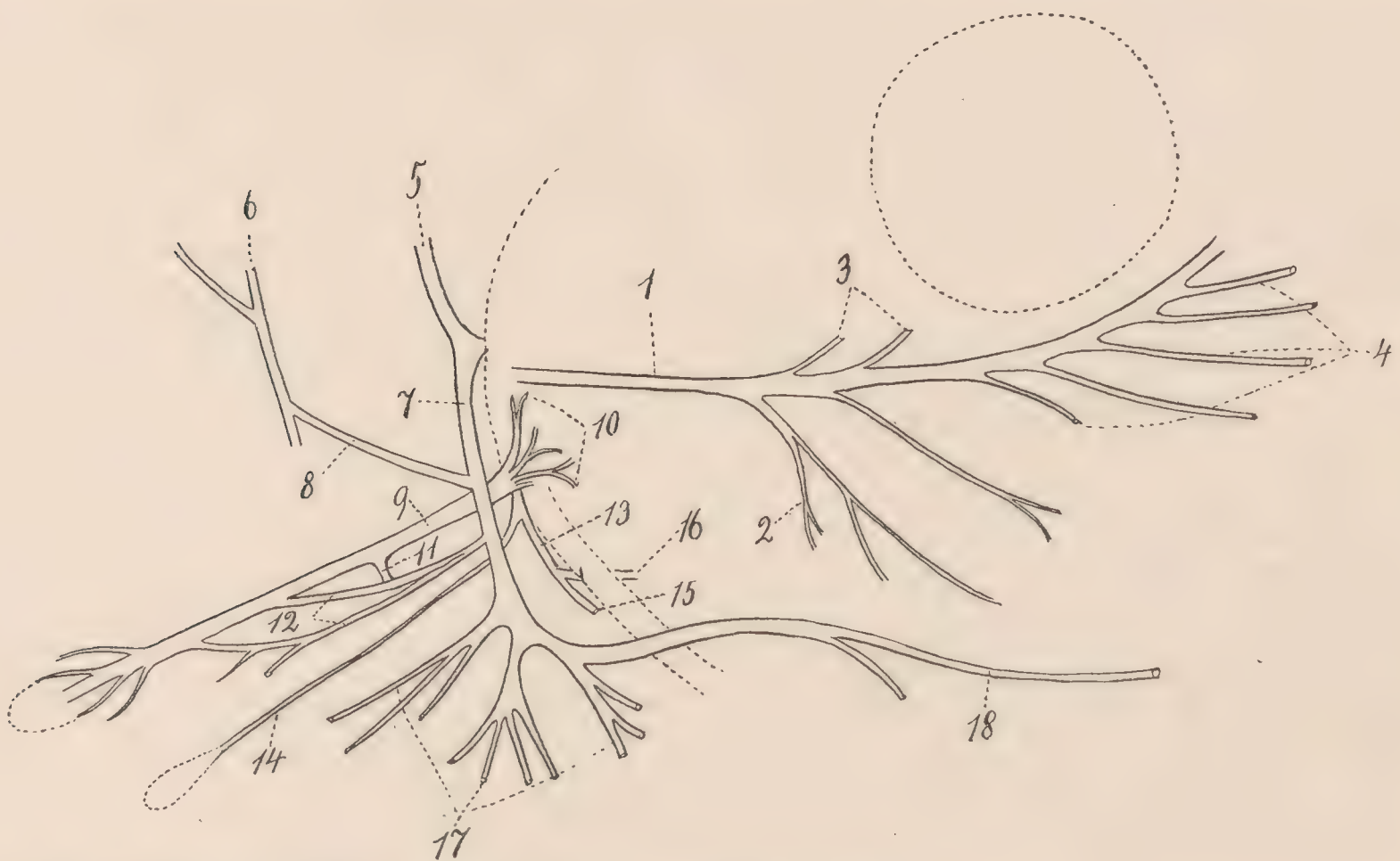


Fig. 17. Schema of the caudal cranial nerves of the right side.

1, Facial nerve; 2, Branch to depressor mandibuli; 3, Branches to obicularis orbitalis; 4, Branches to facial musculature; 5, First cervical nerve; 6, Second cervical nerve; 7, Hypoglossal; 8, Anastomotic branch between second cervical and hypoglossal; 9, Vagus; 10, Accessory branches of vagus to sternomastoid and cephalohumeralis; 11, Superior laryngeal branch of vagus; 12, Anastomotic branches between vagus and hypoglossal; 13, Glossopharyngeal; 14, Branch to innominate artery; 15, Branch to hyoideus latus; 16, Branch to stylopharyngeus and mucus membrane; 17, Branches to infrahyoid muscles; 18, Branches to geniohyoid and genioglossus and hyoglossus muscles.

nerve and is enclosed in the same dural sheath. The two separate on entering the periotic; the facial to enter the facial canal, and the eighth to enter the internal auditory meatus. The eighth ends by dividing into branches which pierce the small foramina in the end of the internal auditory meatus. The seventh, after entering the facial canal in the periotic, following the course of the canal curves slightly caudad, and then, leaving the periotic, comes to lie between the tympano-mastoid and the exoccipital

and emerges upon the surface of the skull through a foramen formed by these two bones, mesial to the attachment of the stylohyal to the skull. It passes rostrad close to the skull, at first ental to the sternomastoid and cephalo-humeralis, and then beneath the mass of fat and connective tissue underlying the panniculus. It continues forward ventrad to the orbit and ental to the superficial facial muscles. There it turns dorsad and mesad to enter the region of the spiracular sac through the antorbital notch and ends by breaking up into branches supplying the musculature of this region.

It sends a branch to the panniculus in the region of the lower jaw. A small branch supplies the depressor mandibuli. Branches are given off to the facial muscles and the obicularis palpebrarum, and terminal branches supply the musculature of the spiracular sac.

An inspection of Le Danois' figures makes it evident that it is the trunk of the facial nerve which he has described as the fibrous zygomatic process.

The glossopharyngeal and the vagus nerves leave the cranial cavity through the posterior part of the jugulo-acoustic foramen. They pass ventrad, lying in a groove, or better a canal, formed by the otocranial process of Owen, the exoccipital, and the periotic. Reaching the notch between the ventral borders of the first two of the above mentioned bones, the nerves turn sharply caudad and appear in the cervical region.

The glossopharyngeal lies ventral and a little mesial to the vagus. It passes ventrad close to the stylohyal cartilage and gives off a branch which passes caudad lying ventral to the great vessels of the neck. This branch ends by breaking up into a plexus on the surface of the innominate artery. The main trunk curves rostrad, giving off a branch to the hyoideus lateralis, and passes deep to the stylohyal. Here it gives off a branch to the stylopharyngeus. It then continues forward, lying deep to the palate muscles, and ends by supplying the mucus membrane of the soft palate and fauces, and also the posterior portion of the tongue.

As in *Balænoptera*, the vagus is intimately associated with the sympathetic. It appears in the neck ventral to the attachment of the styloid process and gives off branches to the sternomastoid and mastohumeralis. These are no doubt equivalent to the spinal accessory of other animals. Close to this, the vagus is crossed by and is adherent to the hypoglossal. In its course caudad, the nerve lies close to the ventral border of the middle scalene and dorsal to the great arteries. The superior laryngeal nerve arises near the junction with the hypoglossal, passes mesad until it reaches the fascial plane deep to the great vessels, and there turns ventrad to reach the larynx.

In its course the vago-sympathetic trunk received two fine branches from the hypoglossal. Just before reaching the subclavian artery it sepa-

rates into its vagal and sympathetic components. On the right side, the vagus crosses the vessels in several separate strands. Small anastomotic connections unite these with the plexus formed by the glossopharyngeal. The smaller strands pass down along the aorta. The largest division, after sending several cardiac branches to the aorta, turns mesad and dorsad behind the tracheal bronchus to reach the root of the lung, where it forms the posterior pulmonary plexus. Before this it gives off a branch which passes in front of the bronchus, forming the anterior pulmonary plexus and anastomosing with the cardiac plexus. The strands of the posterior pulmonary plexus unite upon the œsophagus and pass caudad upon its dorsal surface.

The left vagus differs from the right in that its sympathetic element is more distinct. The first branch after the separation of the sympathetic element is much larger than on the right side and passes to the ventral surface of the aorta, forming with the branches from the right side and some fibers from the sympathetic the cardiac plexus. The main vagal trunk gives off an anterior pulmonary branch, as on the right side, and then, as it passes the ductus in its dorsal course, it sends a small nerve cephalad behind the aorta toward the larynx. This probably is the recurrent laryngeal. It was not found on the right side. The posterior pulmonary plexus was formed as on the right side.

The hypoglossal nerve emerges from the hypoglossal canal. This is widely separated from the jugular foramen and opens upon the caudal surface of the skull. On exit, the nerve receives a large anastomotic branch from the first cervical. The resultant trunk passes ventrad, lying at first in relation to the exoccipital and then to the stylohyal. The scale-nus medius lies ental, the sternomastoid and mastohumeralis ectal, to it. A short distance from the point of emergence, it receives an anastomotic branch from the second cervical. Then it crosses the vagus, lying ectal and closely adherent to the latter. Slightly further ventrad, it crosses the great vessels and leaves the stylohyal. It is covered in this region by deep fascia and panniculus. Here two small branches pass caudad to anastomose with the vagus. The next branches are given off to the sternothyroid and the sternohyoid muscles. The trunk then arches rostrad along the dorsal border of the sternohyoid, giving off large branches to the deep surface of this muscle and to the thyrohyoid. Crossing the border of the thyrohyal cartilage, it turns rostrad and mesad, and, for a short distance, lies between the stylohyal and the thyrohyal cartilage upon the ceratohyal muscle. It then ramifies upon the hyoglossus muscle. The mylohyoid is at this point superficial to the nerve. The hypoglossal ends by breaking up into branches supplying the geniohyoid, the hyoglossus, and the genio-glossus muscles.

The plexus formed by the cervical nerves in *Kogia* is characterized by the formation of two large masses of nerve fibers. These, for purposes of convenience, have been termed the lesser brachial trunk and the greater brachial trunk. The former is produced by the union of two cords comprised of the third and fourth, and fifth and sixth cervical nerves respectively. The latter is formed by a large band of fibers from the lesser brachial trunk and two cords from the seventh and eighth cervical nerves, assisted by the first thoracic.

This condition has not before been described and it is very different from the arrangement pictured by Cunningham¹ in *Phocæna*. In that animal, the innervation of the flipper takes place through a single trunk formed from the last five cervical and the first thoracic nerves, but the conspicuous division of the cervico-brachial trunk above mentioned is absent. The plexus of *Balænoptera* suggests the condition but is by no means as definite.

The arrangement, so far as it goes, would tend to place *Kogia* somewhat nearer to the mystacocetes than to the Delphinidæ — an inference which receives further support from the arrangement of the antebrachial musculature.

The cervical nerves, with the exception of the first, possess ventral and dorsal divisions, the separation occurring in the vertebral foramina. The dorsal divisions will be considered separately. The first cervical nerve emerges from the spinal canal, between the atlas and the occiput. Its point of exit is separated from the other cervical nerves by a considerable interval and is dorsal to the lateral mass of the atlas. In its course ventrad and slightly rostrad, it gives innervation to the rectus posticus, rectus lateralis, rectus anticus, and superior oblique muscles. It ends by anastomosing with the hypoglossal near the point of emergence of the latter nerve. The other cervical nerves leave the spinal canal very close together. The second cervical nerve emerges singly and gives off a small branch which passes rostrad, lying upon the rectus anticus, and unites with a branch of the first cervical upon the surface of that muscle. The nerve continuing soon unites with the third and fourth. These latter emerge closely approximated and fuse almost immediately into a single trunk. The connection between this trunk and the second cervical is only temporary; for the resultant nerve mass, after giving off a branch to innervate the scalenus medius, separates into two large nerves which pass ectad between the scalenus posticus and medius.

The first of these two nerves is probably derived mainly from the second cervical. It passes ventrad and rostrad, ectad to the scalenus medius, and

¹ Cunningham, D. J. Jour. Anat. & Phys., XI, 1876-77.

breaks up to supply the tissues of the neck, the cervical panniculus, and the overlying skin. In its course, it gives off a branch which, by uniting with twigs from the third, fourth, fifth, and sixth, forms a nerve to innervate the levator anguli scapulæ and the rhomboideus capitis. There is a large anastomotic branch which connects with the hypoglossal and represents the ansa hypoglossi. Just before the nerve breaks up, it sends a division to anastomose with a branch from the lesser brachial trunk, the combination serving to innervate the upper portion of the pectoralis major.

The portion composed for the most part of the third and fourth cervical nerves passes ventrad and slightly caudad, giving off branches to the middle scalene muscle, and ends by fusing with a cord formed by the fifth and sixth cervical to produce what is termed the lesser brachial trunk. The fifth and sixth cervical unite very soon after emergence from the vertebral canal. They probably receive sympathetic branches before fusion, but this was not definitely ascertained. The resulting cord passes ventrad and caudad, lying ectal to the scalenus medius. This cord gives twigs as above noted which assist in innervating the levator anguli scapulæ and finally, ental to the scapula, unites with the cord composed of the third and fourth. The resultant brachial trunk gives off a branch (*vide supra*) which assists in the innervation of the pectoralis major. The next branch is the suprascapular nerve. This is large and proceeds to the ectal surface of the scapula. Here it ramifies upon the deep surface of the deltoid, supplying it together with the subdeltoideus, the infraspinitus, and the supraspinatus. It anastomoses with branches of the circumflex nerve. The phrenic nerve arises from the lesser brachial trunk near the foregoing. It passes ventrad and then, as it reaches the border of the scalenus medius, it turns caudad to accompany the great vessels into the thorax. At this point it gives off a branch to the pectoralis minor. From the ectal surface of the lesser brachial trunk there are given off four or five small branches which enter the subscapularis muscle to supply it. Lastly, the major portion of the lesser brachial trunk passes caudad and ventrad to unite with the cords of the seventh and eighth cervical to produce the greater brachial trunk.

The seventh and eighth cervical communicate with the sympathetic and give off branches supplying the scalenus posticus muscle. The seventh cervical sends a branch to supply the longus colli. The two nerves unite after this and form a single cord. This, lying ental to the scalenus medius, divides into two parts. The most superficial portion gives off a branch which pierces the muscle and passes caudad to supply the serratus anticus. Then it pierces the scalenus medius itself and unites with the continuation of the lesser brachial trunk. The deeper portion receives a large addition from the first thoracic nerve and then, near the ventral border of the scale-

nus medius and just cephalad to the first rib, pierces the muscle and unites with the anastomosis between the superficial portion and a branch from the lesser brachial trunk (Fig. 18.38). This is broad and flat, and lies ental to the scapula near the scapulo-humeral articulation.

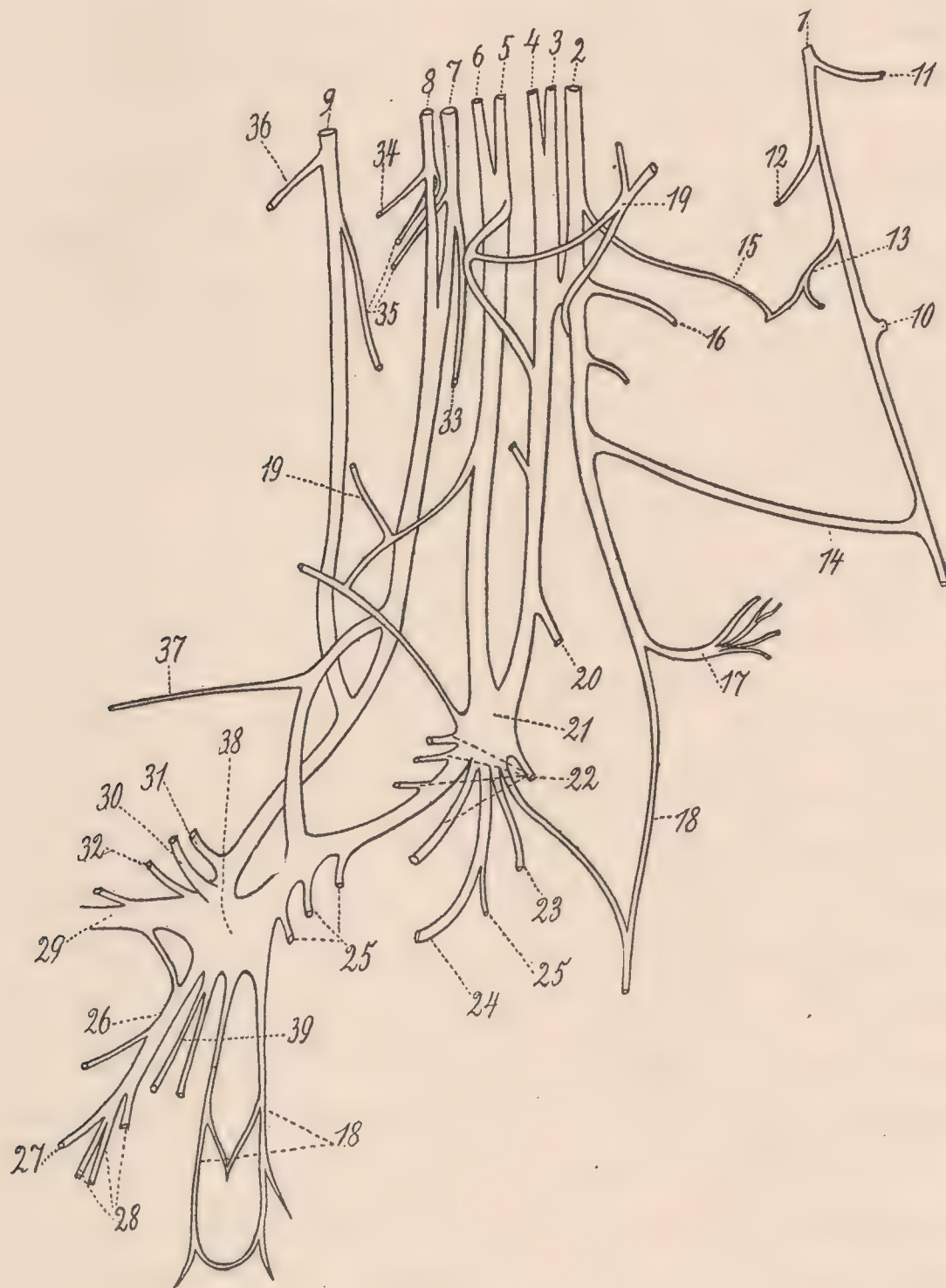


Fig. 18. Cervico-brachial plexus, ventral divisions.

1, First cervical nerve; 2, Second cervical nerve; 3, Third cervical nerve; 4, Fourth cervical nerve; 5, Fifth cervical nerve; 6, Sixth cervical nerve; 7, Seventh cervical nerve; 8, Eighth cervical nerve; 9, First thoracic nerve; 10, Hypoglossal nerve; 11, Branch to rectus posticus; 12, Branch to rectus lateralis; 13, Branch to rectus anticus; 14, Anastomotic branch to hypoglossal; 15, Branch to rectus anticus; 16, Branch to scalenus medius; 17, Branch to panniculus; 18, Branch to pectoralis major; 19, Loop supplying levator anguli scapulæ and rhomboideus; 20, Branch to panniculus; 21, Lesser brachial trunk; 22, Branches to subscapularis; 23, Suprascapular nerve; 24, Phrenic nerve; 25, Branch to pectoralis minor; 26, Ulno-median nerve; 27, Musculo-spinal nerve; 28, Ulnar nerve; 29, Long thoracic nerve; 30, Circumflex nerve; 31, Nerve to teres major; 32, Branch to panniculus overlying scapula; 33, Nerve to longus colli; 34, Scalenus posticus; 35, Connections between sympathetic, seventh and eighth cervical, and first thoracic; 36, Intercostal portion of first thoracic; 37, Nerve to serratus anticus; 38, Greater brachial trunk; 39, Cutaneous nerves to radial margin of flipper.

From the anterior part of this trunk three or four small nerves (25) arise which supply the pectoralis minor. Next to these there is a double

loop (18), as shown in the diagram, which innervates the greater portion of the pectoralis major. In conjunction with the origin of the loop, a nerve passes (39) distad, crossing the ental surface of the flipper just below the tuberosity of the humerus to reach the radial border. More distal to, paralleling, and connected with the above is another rather larger nerve which disappears under the dense tissue forming the origin of the flexor muscles. Near the origin of these two nerves, the circumflex nerve (30) arises and passes ectad in the space between the teres and the scapulo-humeral articulation, and ends by anastomosing with the suprascapular nerve to take part in the supply of the deltoid. Next in order, a single large nerve (26) arises from the distal portion of the trunk and continues along the postaxial border of the flipper upon the flexor surface. Near its origin, it gives off an anastomotic branch to the long thoracic. Just distal to this, there is a large branch (27) which pierces the triceps, innervating that muscle, and then curves around the postaxial border just proximal to the olecranon to reach the extensor surface of the flipper. Here it ramifies on the ental surface of the extensor digitorum, supplying this muscle. This corresponds to the musculo-spiral nerve.

The main nerve passes distad on the flexor surface of the flipper, dividing into five or six branches (28) which ramify underneath the flexor muscle and supply it. The two branches near the postaxial border supply the interossei. This nerve probably represents the combined ulnar and median.

From the caudal extremity of the greater brachial nerve arises the long thoracic nerve (29). It passes caudad, lying at first in relation to the subscapularis muscle and receiving anastomotic branches from the ulnar median complex. Near its origin, it gives off a large branch (23) which curves around the border of the scapularis and then ramifies in five or six divisions upon the ental surface of the panniculus, supplying the dorsal portion of that muscle from the scapular region almost to the caudal extremity.

The long thoracic is continued caudad beneath the fibrous raphe of the panniculus and forms a plexus with branches of the segmental nerves from the first to the eleventh thoracic. This plexus is composed of from two to four parallel nerves, connected by anastomoses and giving off branches supplying both dorsal and ventral portions of the panniculus. This plexus ends with the panniculus.

From the ectal surface of the greater brachial trunk, the nerve (31) to supply the teres major arises. Near its ending in that muscle it sends a branch caudad to supply the latissimus dorsi.

The dorsal divisions of the cervical nerves separate from the ventral divisions in the vertebral foramina and emerge so close together that it is

practically impossible to distinguish them from one another. They pass dorsad between the atlas and the transverse process of the first thoracic vertebra and ramify in tree-like arborizations to supply the dorsal musculature. The various branches anastomose with one another. Some medial branches to the semispinalis capitis extend caudad in the substance of that muscle as far as the fourth and fifth thoracic vertebra. A branch from one of the lower members of the plexus connects it with the dorsal division of the first thoracic nerve across the transverse process.

The thoracic nerves emerge from the intervertebral foramina as single

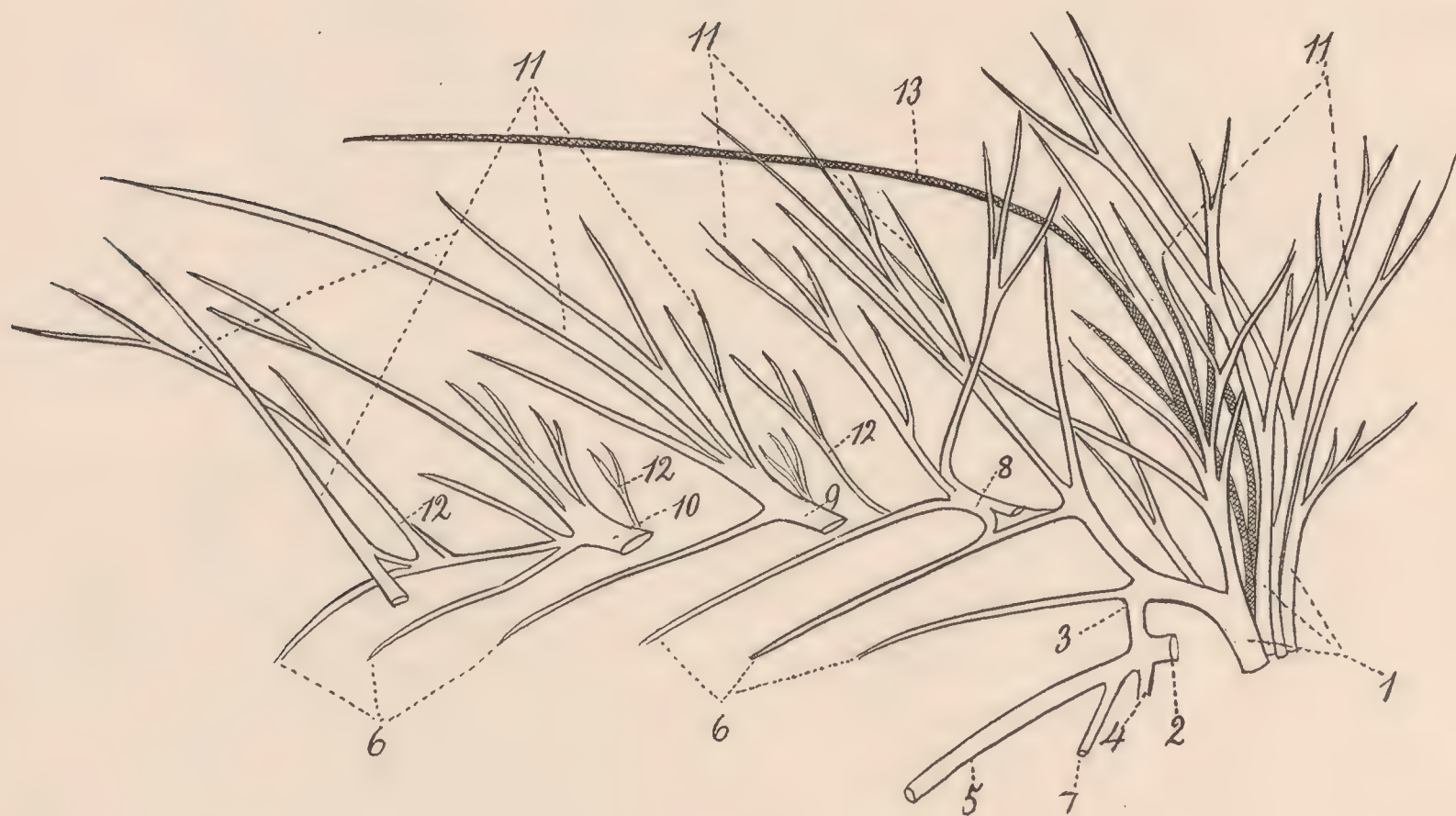


Fig. 19. Dorsal divisions of cervical and upper thoracic nerves.

1, Dorsal branches of last seven cervical nerves; 2, First thoracic nerve; 3, Dorsal division of first thoracic nerve; 4, Branch to cervico-brachial plexus; 5, Intercostal branch of first thoracic; 6, Branches of dorsal divisions to transversarius; 7, Branch of first thoracic to sympathetic; 8, Dorsal division of second thoracic; 9, Dorsal division of third thoracic; 10, Dorsal division of fourth thoracic; 11, Branches to longissimus; 12, Branches to multifidus and erector spinae; 13, Branches to semi-spinalis capitis.

trunks and separate into dorsal and ventral divisions between the transverse processes. The ventral portion lies, throughout the greater part of its course, between the pleura and the intercostal muscles, at first lying near the rib next below but soon crossing the intercostal space to lie near the rib just above. Near its origin, it sends off a collateral branch which ramifies between the two layers of intercostal muscles supplying them. As the nerve nears the level of the lateral raphe of the panniculus, it sends a branch which pierces the intercostal muscles to unite with the long thoracic of the brachial plexus to form the plexus supplying the panniculus. The ventral division ends by ramifying in and supplying the rectus abdominis.

The ventral division of the first thoracic nerve differs from the other members in that it gives off, at the region of its first or intercostal branch, two other branches. The larger of these pass cephalad and ventrad beneath the first rib to join the deep cord of the seventh and eighth cervical and enter into the formation of the brachial plexus. The smaller branch crosses the dome of the pleura to reach the tip of the second ganglion of the cervical sympathetic system.

The dorsal divisions pass between the transverse processes and separate into three main divisions. The most mesial of these pass caudad and dorsad to the interspinous space next below to supply the multifidus. In the mid-thoracic region the spinalis dorsi also receives branches from this set. The second set are more numerous and much larger and ramify in the substance of the longissimus, supplying it, and the iliocostalis. The third set are distributed to the transversarius, their cutaneous branches emerging through the lateral intermuscular septum.



Fig. 20. Schema of lumbo-sacral nerves.

1 to 9, Lumbo-sacral nerves, in order; 10, Last thoracic nerve; 11, Nerves from dorsal divisions supplying longissimus and iliocostalis muscles; 12, Nerves from dorsal divisions supplying multifidus and interspinalis muscles; 13, Nerves from dorsal divisions supplying transversarius; 14, Dorsal longitudinal trunk; 15, Ventral divisions; 16, Branches of abdominal muscles; 17, Anastomotic branch from fifth to sixth lumbo-sacral nerve; 18, Internal pudic nerve; 19, Ventral longitudinal trunk.

The lumbo-caudal plexus is characterized by the formation of two longitudinal trunks which lie respectively above and below the transverse processes of the vertebræ. This condition obtains in *Phocæna*, according to Cunningham, in a more marked degree, and is probably a result of the arrangement of the muscles going to the pedicle. These trunks are formed by the middle and lower members of the plexus.

Like the thoracic nerves, the lumbo-caudal nerves divide into dorsal

and ventral divisions between the transverse processes of the vertebræ. The dorsal divisions, in arrangement, resemble those of the thoracic nerves. There is present the same separation into three branches. The most internal crosses the adjacent vertebra and the intervertebral space to supply the multifidus and interspinalis, the middle branch enters the longissimus and ilio costalis muscles and the external branch crosses the transverse processes caudad to supply the transversarius.

From the dorsal division of the second nerve of the series, a branch arises which anastomoses with the dorsal division of the next segment. From this, a still larger anastomotic branch passes to the fourth and, increasing in size by successive segmental increments, continues caudad. At first only a portion but further caudad the whole dorsal division enters into the cord, and the three sets of branches already noted arise from this and not from the dorsal nerve before its entrance into the trunk. This trunk was traced as far as the base of the flukes where it was lost.

The ventral divisions pass ectad between the transverse processes and enter into the substance of the hypaxial muscle, first giving off small branches which may be sympathetic in character. The first four pass ventrad, giving off branches to the superficial layer of the hypaxial muscle. These branches turn dorsad in the substance of the muscle. Branches are also given off to supply the internal and external oblique muscles. The nerve ends by supplying the rectus abdominis.

The fifth lumbar nerve, in addition to the usual arrangement, in the substance of the hypaxial muscle sends a large anastomotic branch to join the sixth. The latter, thus reinforced, unites with the seventh of the series and forms the nerve termed by Cunningham the internal pudic. This passes ventrad between the muscle layers to the venter of the animal and ends by breaking up into two main divisions. The anterior of these ramifies and forms a plexus supplying the genital muscles. The posterior branch supplies the anal musculature.

From the ventral divisions of the seventh, before the formation of the internal pudic nerve, a large anastomotic branch passes caudad to unite with the ventral division of the eighth. This is continued as a trunk, lying below the transverse processes, and is joined by the ventral divisions of the succeeding nerves. At the points of junction, branches are given off to the adjacent muscles. This trunk was traced along the ventro-lateral surface of the vertebræ to the base of the flukes. This sustains Cunningham's findings in *Phocæna* and strengthens his argument as to the probable sensibility of the whale's tail as against Swann, who thought there was but little sensation in the flukes.

The sympathetic system is represented in the neck by three ganglia and their connections.

The most rostrad and ventrad of these ganglia is intimately associated with the vagus. On the right, the two are fused. The cephalic connections of the ganglion are represented by a small strand on the surface of the main vagus trunk. On the left side, the ganglion is united with the vagus only by several fibers crossing directly from the body of the ganglion to the nerve. From the superior pole, a large branch connects with the vagus in the region of the superior laryngeal nerve. From the caudal pole, a large nerve connects it with the second ganglion of the series.

The second ganglion is situated cephalad to the apex of the lung. It is

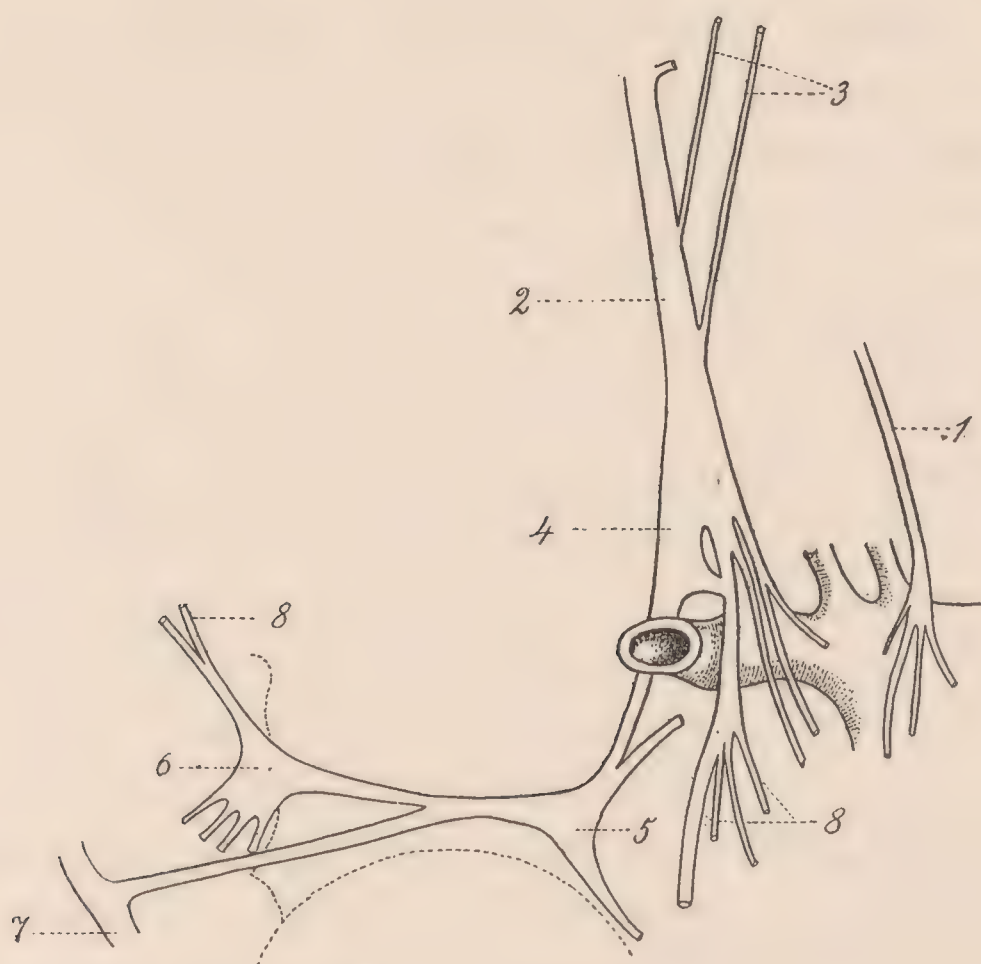


Fig. 21. Cervical sympathetic ganglia.

1, Branch of glossopharyngeal; 2, Vagus; 3, Anastomotic branches from hypoglossal; 4, First sympathetic ganglion; 5, Second sympathetic ganglion; 6, Third sympathetic ganglion; 7, First thoracic nerve; 8, Branches connecting with seventh and eighth cervical.

connected by large trunks with the ganglion just described, and the third of the series. It receives a large contribution from the first dorsal nerve and gives off several small nerves which pass mesad to anastomose in front of the aorta, and assist in the formation of the cardiac plexus.

The third ganglion of the series lies close to the 1st thoracic vertebra. In addition to the connection mentioned above, it receives rami from the various cervical nerves and sends three or four branches rostrad along the vertebral column.

The ganglionic cord lies upon the lateral surface of the vertebral column. It is connected with the cervical sympathetic, as described above, by means of several small strands. It becomes definite at the upper level of the fifth

thoracic vertebra and receives branches from each segmental nerve from the fifth thoracic to the eleventh. Augmented by these branches, it increases in size to the level of the tenth thoracic vertebra where a large nerve is given off. This passes to the root of the mesentry which it enters and represents the splanchnic nerves. The cord from this point on becomes less of a trunk and more of a true ganglionated cord, and lies embedded in the hypaxial musculature.

Article III.—INSECTS OF FLORIDA

V. THE WATER BEETLES¹

BY CHARLES W. LENG AND ANDREW J. MUTCHLER

INTRODUCTION

In the preparation of this list the same authorities have been consulted as in the preparation of the List of Carabidæ of Florida.² These include the Hubbard and Schwarz records of 1878, the subsequent manuscript additions of Mr. Schwarz, the published and manuscript additions of Mrs. Annie Trumbull Slosson, and the results of expeditions to Florida by members of the Museum Staff and other entomologists whose names are mentioned in the text. In addition, the records of the late Mr. C. H. Roberts' Collection (now in this Museum) and those in the collection of Mr. John D. Sherman, Jr., have been incorporated. These two entomologists have, for many years, specialized in aquatic Coleoptera and employed Mr. W. S. Genung to collect Florida Water Beetles. In Haliplidæ, the papers by Dr. R. J. Matheson and Mr. Roberts have been followed; in Dytiscidæ, Mr. Sherman's knowledge of the scattered literature has been helpful; in Hydrophilidæ, the studies of Mr. Fred Wintersteiner, thus far unpublished, have been useful; and in Parnidæ, the unpublished studies of Mr. Harry H. Knight have been of assistance; but, withal, it must be admitted that among the small species there is still some confusion, which we have aimed to clarify as far as possible. The specimens collected by Grossbeck, Leng, Lutz, Mutchler, and Watson are in the collection of The American Museum of Natural History.

In comparison with the water beetle lists of some other section, after making some allowances for the various degrees of completeness with which the material has been worked up, the number of species occurring in Florida may seem small. It is due, in part, to the almost total failure of the great northern genus *Hydroporus*, whose numbers swell the list for any northern locality. Other, smaller but important, northern genera that are missing

¹ The following new names and synonymy are proposed in this paper:

Celina slossoni, new species.

Bidessus shermani, new species.

Halplus confluentus Roberts = *H. havaniensis* Wehncke.

They are to be credited to Mr. Mutchler alone.

² Bulletin American Museum Natural History, XXXIX, 1915, pp. 555-601.

are *Ilybius* and *Agabus*. This difference is most marked in the carnivorous Dytiscidæ,¹ but it is also plainly seen in the Haliplidæ, Gyrinidæ, and Parnidæ. The numbers of the Hydrophilidæ, which though water beetles are not Adephaga, are, however, nearly equal to those of northern regions.

The Number of Species Reported from Various Regions

	N. J.	Ind.	D.C.	S.W. Pa.	Fla.	W.I.
Dytiscidæ	95	69	49	39	42	43
Haliplidæ	10	11	6	2	6	3
Gyrinidæ	25	15	10	6	10	8
Hydrophilidæ	42	39	29	32	39	33
Sphæridiidæ	16	15	17	15	11	13
Parnidæ	18	7	16	10	6	10
	—	—	—	—	—	—
	206	156	127	104	114	110

An effective comparison with the West Indian fauna is not yet possible, since our West Indian list is far from complete; but a total about the same as that recorded for Florida is indicated as probable, with about 20% of identical species. These identical species are partly northern ones which extend through Florida to Cuba or beyond, and partly Antillean species that have been found in Florida. The strong flight of water beetles, coupled with the similarity of some aquatic environments wherever they occur, are doubtless factors that tend to produce this result. It may eventually appear, after a detailed study family by family has been completed, that a greater similarity between the beetles of Florida and Cuba is to be found in the families of water beetles treated in this article than in any other family.

It may be worth noting from our personal experiences that in Florida the water beetles were seldom in its beautiful clear lakes but rather in roadside ditches, shallow rain-pools, etc., in which there was some vegetable growth. One such pool near Punta Gorda was so shallow that it was not everywhere easy to sink the net entirely under the surface but 20 species (nearly a quarter of the whole fauna) rewarded an hour's work. A similar and almost equally productive pool was found about a mile west of Lakeland; and a shallow ditch near Titusville also abounded in specimens, including the rare genus *Ochthebius*. Many of the records from Lake Monroe at Enterprise result from Mr. Brownell's winter sifting of the lake shore debris, and part of the Fort Myers records commemorate the

¹ Sharp (Camb. Nat. Hist. Insects, II, p. 213) has noted the apparently boreal tendency of this family, remarking upon their abundance in Lapland; but in his great Monograph, he points out that this is particularly true for the Dytisci complicati only.

night work of Messrs. Grossbeck and Davis at electric lights. The Lake Okeechobee records that we have from Mr. Blatchley also refer to the fauna of the shores rather than of the depths. Taken together, these data furnish a picture of large numbers of aquatic beetles flying by night in search of new breeding places, where food, inaccessible to terrestrial insects, is to be found for their young.

DYTISCIDÆ

The Water Tigers, as the Dytiscidæ have been called, exhibit the greatest aquatic development of the Adephaga. Their swimming powers are developed in the highest degree and they possess special adaptations in their breathing structures to an aquatic life. They are *the* water beetles par excellence. The larvæ are carnivorous.

Associated with them in this paper, will be found the aquatic Hydrophilidæ, Gyrinidæ, Haliplidæ, and Parnidæ because the adults are usually found in water; also the Sphæridiidæ (which are not aquatic) because their usual position in catalogues adjoins that of the Hydrophilidæ. A discussion of the family relationship and the light that has been thrown thereon from a recent study of genitalia will be found on a subsequent page; here it may suffice to say that we regard the Dytiscidæ as aquatic Adephaga, constituting with Carabidæ, Amphizoidæ, and Cicindelidæ one of the great series of Coleoptera. The highest authority on Dytiscidæ has long been Dr. David Sharp of Cambridge, England, and his ideas, in part made known to us by Mr. Sherman, have been largely followed in our arrangement of the species. As far as we have been able to determine them, they are briefly described in the following pages.

DYTISCI FRAGMENTATI

NOTERINI

Notomicrus nanulus (Leconte)

Elongate oval. Head, thorax, and antennæ reddish yellow. Elytra dark reddish brown, apex slightly attenuate. Under side of the same color as head and thorax. Length, 1.25 mm.

Crescent City and Bartow (Schwarz); Dunedin, January to March (Blatchley); Bartow, July (Roberts Coll.). Described from Louisiana: rare.

SUPHISINI

Colpius inflatus Leconte

Globose, obtusely acuminate behind. Opaque black. Antennæ and legs rufous. Upper surface obscurely variegated with red. Head (beneath) and sides of thorax reddish. Elytra strongly punctate. Body opaque beneath. Coxæ with a few large scattered punctures; abdomen impunctate; apical margin setose. Length, 3.5 mm.; width, 2.5 mm.

Tampa, rare, and St. Augustine (Schwarz); Jacksonville and Taylor Co., July (Genung in Leng Coll.); Enterprise, November (Brownell in Leng Coll.); Dunedin, Kissimmee, and Lake Okeechobee, January to March (Blatchley); Jacksonville, June and July (Roberts Coll.). Described from Louisiana. Crotch gave the distribution as Louisiana, Florida, and New York, but the last is certainly erroneous.

HYDROCANTHINI

Hydrocanthus iricolor Say

Ovate, convex, attenuate behind. Head, thorax, and under surface reddish yellow. Elytra dark reddish brown polished, iridescent with three visible rows of fine dorsal punctures. Prosternal process very broad behind the coxæ. Hind tibiæ broad. Length, 4-5 mm.

Lake Harney, Tampa, St. Augustine, Crescent City, and Bartow (Schwarz); Lakeland, November (Davis); Gainesville, September and October (Mutchler and Watson); Dunedin, Kissimmee, Lake Okeechobee, and Sarasota, January to March, common (Blatchley). Recorded also from Guadeloupe. None in Roberts Coll. Crotch gave the distributions as Pennsylvania, Georgia, and Louisiana. The type locality is not given in the original description.

Hydrocanthus oblongus Sharp

Reddish brown. Elytra somewhat shining, almost impunctate. Prosternal process deeply hollowed out and nearly impunctate in the male; in the female it is flat and variably punctured. Hind coxal plate somewhat coarsely and closely punctured. Ventral segments smooth, shining. Length, 4 mm.; width, 2 mm.

Common in Florida (Sherman); Marion Co., Hastings, Sanford, and Jacksonville (Amer. Mus. Coll.); Enterprise, October to December (Brown-

ell); Fort Myers, November, and Titusville, November (Lutz); Taylor Co., July and August, Sanford, February, Jacksonville, August (Roberts Coll.). The original description merely mentions North America as the locality. Blatchley records *atricolor* from Sanford, January, and Lake Okeechobee, March, but we believe his record also refers to *oblongus* or *texanus*.

Hydrocanthus texanus Sharp

Oval, convex, shining. Dark ferruginous. Elytra iridescent black. Under side with posterior part darker. Length, 4.25 mm.; width, 2.25 mm. This species is darker and comparatively more convex than either of the two former species, and in respect to the elytral punctures is intermediate between the two.

Jacksonville, July (Roberts Coll.). Described from Texas.

A species of *Hydrocanthus*, doubtfully identified by Mr. Schwarz as *atricolor* Say (which, according to Crotch, was described from Mexico), or *texanus* Sharp, was found at Lake Harney.

Canthydrus floridanus Blatchley

Short ovate, strongly convex. Head and thorax reddish yellow with a black or fuscous cloud on the occiput and middle or apical half of the thorax. Elytra dark brown. Antennæ, under surface, and legs pale reddish yellow. Head and thorax without punctures, except for a few coarse ones on the basal half of the latter. Elytra with numerous irregularly placed, very shallow punctures. Length, 2-2.2 mm.

Described from Kissimmee, beneath rubbish, and Lake Okeechobee, February and March (Blatchley).

Canthydrus puncticollis (Crotch)

Head, thorax, antennæ and under side testaceous. Thorax with more or less distinct infusate mark on the middle at the apex; punctation visible only on the basal portion. Elytra piceous with an irregular testaceous mark in front of the middle, starting at the side but not reaching the suture; coarsely and somewhat closely punctate. Length, 3 mm.

Enterprise (Schwarz); Jacksonville, August (Roberts Coll.). These records antedate the description of *floridanus* and may refer to that species. The type locality is not given in the original description.

Canthydrus bicolor (Say)

Ovate, convex. Head, thorax and under side reddish yellow. Elytra dark reddish-brown, closely and somewhat coarsely punctate. Length, 2.5 mm.

Lake Harney, Tampa, St. Augustine, and Bartow (Schwarz). Described from Louisiana. Crotch gave distribution as Pennsylvania and Florida. No specimens from Florida in the Roberts Collection.

Canthydrus gibbulus (Aubé)

Ovate convex. Head and thorax yellow, the latter clouded with dusky on the apical margin. Elytra piceous or dark brown, with an oblique, irregular, yellowish cross-bar near the middle, less closely punctate than in the preceding and with the dorsal rows of punctures more distinct. Length, 2.5 mm.

Lake Worth and Biscayne Bay, January to March (Slosson Coll.); Sarasota, Dunedin, Kissimmee, Fort Myers, and Lake Okeechobee, January to March, very common (Blatchley); Punta Gorda, November (Davis); Sanford and Jacksonville (Amer. Mus. Coll.); Enterprise, December, in lake shore debris (Brownell in Leng Coll.); Punta Gorda and Fort Myers, November, in shallow grassy pools (Lutz, Davis, and Leng). Sanford, February; Taylor Co., July; and Jacksonville, August (Roberts Coll.). The original description merely gives the United States as the locality.

LACCOPHILINI

Laccophilus pumilio Leconte

Ovate, pointed behind, not convex. Unpunctured. Rufo-testaceous, meso- and metasternum darker. Elytra piceous, slightly iridescent, regularly narrowed behind, not obliquely truncate at tip. Abdomen without the distant fine oblique lines seen in the other species. Sharp says: "Very careful examination shows in certain lights traces of two or three lines on the second ventral segment towards the sides, but these are the only evidences of the characteristic ventral sculpture of the other species." Length, 1.9 mm.

Enterprise; the type and only known specimen taken by Mr. Schwarz (Sherman).

Laccophilus gentilis Leconte

Oval, angustate, subdepressed. Shining, rufo-testaceous, thorax at middle of apex and base darker. Elytra finely and closely punctate, fuscous with vague reddish markings. Ventral segments with conspicuous scratches. Front and middle tarsi of male thicker than in female. Length, 3.5 mm.; width, 1.85 mm.

Lake Worth (Slosson Coll.); Crescent City (Schwarz); Sarasota, March (Blatchley); Enterprise, December, in lake shore debris (Brownell in Leng Coll.); Gainesville, September and October (Mutchler and Watson); Crescent City and Taylor Co., July, and Jacksonville, June (Roberts Coll.). Described from Louisiana.

Laccophilus proximus Say

Ovate, narrowed behind; nearly uniform reddish brown. Elytra with traces of greenish yellow spots. Body beneath reddish brown. Length, 4.5 mm.

Jacksonville, Crescent City, Tampa, and Enterprise, common (Schwarz); Dunedin, Sarasota, and Arch Creek, January to March, common (Blatchley); Lakeland, Punta Gorda, Enterprise, and Fort Myers, November (Lutz, Davis, and Leng); Gainesville, September and October (Mutchler and Watson); Jacksonville, July and August, Sanford, April, Taylor Co., August, and Hastings (Roberts Coll.). Described from South Carolina. Crotch gave distribution as Canada, Illinois, Iowa, Nebraska, Texas, and Florida. *L. americanus* Aubé, known from Cuba, Porto Rico, Guadeloupe, and Antigua, does not differ.

There are four other species of *Laccophilus* known from the West Indies which have not yet been sufficiently compared with the Floridian *pumilio* and *gentilis*.

DYTISCI COMPLICATI

HYDROVATINI

Hydrovatus compressus Sharp

Broadly ovate, convex. Piceous. Head and thorax reddish; thorax with base slightly darker, sparsely punctate, coarser and more dense towards the base. Elytra moderately, coarsely and evenly punctate, slightly finer towards the apex. Antennæ and legs rufous. Posterior coxal plate closely and coarsely punctate. Length, 2.3 mm.; width, 1.5 mm. Allied to *Hydrovatus caraibus* Sharp from the West Indies.

Biscayne Bay, January to March (Slosson Coll.); Florida (Blatchley); Enterprise, November and December, in lake shore debris (Brownell in Leng Coll.); Punta Gorda, November (Lutz, Davis, and Leng); Sarasota and Lake Okeechobee, February and March (Blatchley); Jacksonville, July and August, Sanford, February, Taylor Co., July (Roberts Coll.). Described from Louisiana.

BIDESSINI

Desmopachria granum (Leconte)

Short, ovate. Rufo-piceous, shining, sides slightly margined. Thorax finely and sparsely punctate. Elytra finely punctate. Under side finely and sparsely punctate. Length, 1.30–1.65 mm.; width, .80–1.15 mm.

Tampa, Lake Harney, Bartow, and Centreville (Schwarz); Taylor Co. (Leng Coll.); Jacksonville, November (Lutz, Davis, and Leng); Dunedin, February and March (Blatchley); Taylor Co., July (Roberts Coll.); Monticello, October (Mutchler and Watson). Described from Louisiana. Crotch gave Southern States as habitat.

Bidessus fuscatus (Crotch)

Crescent City and elsewhere, common (Schwarz); Lakeland, November (Davis); Titusville, November (Lutz). Taylor Co., July, Lake Worth, and Jacksonville, August (Roberts Coll.). Crotch, in the original description, says it occurs from Lake Superior to Florida.

Bidessus granarius (Aubé)

Cited from northern Florida, but unseen, in Hubbard and Schwarz list. Jacksonville, August (Roberts Coll.). Confirmed by specimens found by C. W. Johnson at St. Augustine, identified by Dr. John Hamilton. Crotch gave Southern States. Aubé mentions merely the United States as the type locality of this and the other species of *Bidessus* which were described by him.

Bidessus exiguus (Aubé)

Lake Harney, Enterprise, Tampa, and Bartow (Schwarz); Belleair, January to March (Slosson Coll.); Jacksonville and Marion Co. (Sherman); Jacksonville (Leng Coll.); Enterprise, November, in lake shore debris (Brownell in Leng Coll.); Dunedin, January to March, common (Blatchley); Jacksonville, August and Lake Harney, March (Roberts Coll.). Occurs also at Valdosta, Ga. (Sherman).

Bidessus seminulum (Leconte)

Enterprise and Crescent City (Schwarz); Crescent City (Roberts Coll.). Described from Florida.

Bidessus pulicarius (Aubé)

(Including *inconspicuus* Leconte as a synonym). Crescent City, Kissimmee, Enterprise, Centreville, Tampa, and St. Augustine (Schwarz); Biscayne Bay, January to March (Slosson Coll.); Tampa, Lake Worth, and Jacksonville (Roberts Coll.); Lakeland, November (Davis); Enterprise, November, in lake shore debris (Brownell in Leng Coll.); Punta Gorda, November, in shallow grassy pools (Lutz, Davis, and Leng); Sarasota, Dunedin, and Arch Creek, January to March (Blatchley); Monticello, October (Mutchler and Watson). Crotch gave Southern States; South Carolina for *inconspicuus*.

Bidessus affinis (Say)

Haulover, Enterprise, St. Augustine, Jacksonville, Biscayne Bay, Lake Worth, and Lake Ashby¹ (Schwarz, including Castle and Laurent and Slosson records); Punta Gorda, November (Lutz, Davis, and Leng); Arch Creek, Bassenger, February to March (Blatchley). None in Roberts Coll. The type locality is not mentioned in the original description, but Crotch gave Atlantic region as habitat.

Bidessus lacustris (Say)

Dunedin and Kissimmee, February and March (Blatchley). Jacksonville, August, and Taylor Co., July (Roberts Coll.). Described from Pennsylvania. Mr. Sherman has not recognized this species in his Floridian material, but has the species from Vowell's Mill, La., and Brownsville, Alpine and Del Rio, Texas. According to Crotch, it is abundant in the Atlantic region.

Bidessus floridanus Fall

Jacksonville and Dunedin, are the type localities. (See Journ. N. Y. Ent. Soc., XXV, 1917, p. 168.)

¹The records for this locality were copied from Mr. Schwarz's paper on the Coleoptera of Florida (Proc. Amer. Philos. Soc., XVII, 1878, pp. 353-472). They probably refer to the Lake Ashley located in the southern part of Volusia County.

Bidessus shermani, new species

Oblong oval; shining, reddish brown. Head and thorax slightly paler than the elytra. Head obsoletely, very finely, and sparsely punctate; with a pair of impressions on the front between the eyes. Antennæ of the same color as the head. Thorax coarsely and densely punctured, and with an impressed line parallel to the apical margin; basal plica extending about half way to the apex. Elytra with the thoracic plica continued on the base but distinctly shorter than the thoracic part; moderately, finely punctate; pubescence very fine, scarcely visible on the basal portion, slightly more dense on apical part; an indistinct groove on the disk beginning at the base and becoming almost entirely obliterated at the apical third. Under side punctate and slightly pubescent; hind coxal plates shining, very sparsely punctate; first ventral segment with a row of slightly coarser punctures at base and apex. Punctures on segments 2 to 5 more or less arranged in rows running parallel with the sutures. Last segment about as broad as the three preceding taken together; with a slight, punctured impression on each side near the base, and with the punctures slightly more prominent on the apical part of the segment. Legs of the same color as the under side. Length, 1.75 mm.; width, about .75 mm.

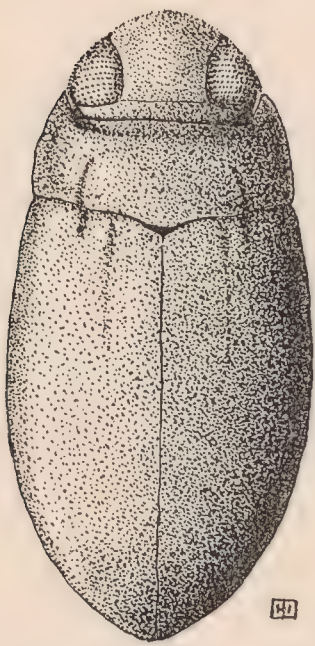


Fig. 1. *Bidessus shermani* Mutchler

Habitat:—Jacksonville (type locality), August 1902, Taylor County, July 1903, and Lake Worth, Florida. Type, No. 24282; paratypes, Nos. 24283, 24284, and 24285.—The American Museum of Natural History.

In the numerous specimens examined there seems to be very little variation, except that the color of the under side of some specimens is slightly darker than in others and the groove of some of the specimens is more noticeable.

This new species differs from *exiguus*, *granarius*, and *lacustris* by the extremely short and indefinite prolongation of the thoracic plica on the basal portion of the elytra, approaching *seminulum* in that respect; while finely pubescent towards apex, it lacks the evident pubescence of *pulicarius*; the elytra show little trace of the elongate markings of *affinis* and are less coarsely punctate than in *fuscatus*; the elytral portion of the plica is also shorter than in any of the above. It differs, finally, from *seminulum* in color, in pubescence, and in size.

Dedicated to Mr. John D. Sherman, Jr., in recognition of much help from him in the preparation of this paper.

The Floridian species of *Bidessus* may be separated by the following key:

1. Basal thoracic plica continued on the elytra.....2.
- Basal thoracic plica not continued on the elytra.....8.

2. Elytral portion of basal plica distinctly longer than the thoracic portion....3.
Elytral portion of basal plica not distinctly longer than the thoracic portion..5.
3. Basal plica not continued to middle of the elytron.....4.
Basal plica elevated and continued beyond the middle of the elytra, forming an
elongate carina; elytra coarsely punctate, not pubescent. (1.65 mm.).
exiguus.
4. Body ovate; elytra coarsely and distinctly punctate; indistinctly pubescent.
(1.75 mm.).....*granarius*.
Body elongate oval; elytra finely and indistinctly punctate; finely pubescent.
(1.4-1.8 mm.).....*lacustris*.
5. Elytra not or very finely pubescent.....6.
Elytra distinctly pubescent with longer yellowish hairs behind the middle and
near the apex. (1.5-1.7 mm.).....*pubicarius*.
6. Elytra finely punctate.....7.
Elytra coarsely punctate, punctures moderately closely placed; coxal plates
with coarse punctures; first and second ventral segments coarsely but sparsely
punctate. (1.7-2 mm.).....*fuscatus*.
Punctures of elytra more closely placed and slightly finer; coxal plates with a
few fine punctures; abdomen with some coarser punctures toward the base.
(1.75-2 mm.).....*floridanus*.
7. Elytra fuscous brown, often with paler, elongate markings; pubescence very
slight, nearly nude. (1.5-1.8 mm.).....*affinis*.
Elytra reddish brown with indistinct fuscous markings; finely pubescent,
slightly more distinct on apical portion. (1.75 mm.).....*shermani* n. sp.
8. Elytra rufo-testaceous; not pubescent, shining, finely punctate. (1.3 mm.).
seminulum.

The two species of *Bidessus* recorded from the West Indies (Cuba and Haiti) have not yet been compared with the Floridian species.

HYDROPORINI

Cœlambus princeps Blatchley

Broadly oval, subdepressed above, strongly convex beneath. Head, elytra, and narrow front and hind margins of thorax dark reddish or piceous brown. Under surface and legs pale reddish brown. Antennæ and legs paler. Eyes very finely granulate. Head and thorax finely, sparsely and irregularly punctate; elytra a little more coarsely, more regularly, and aciculate punctate; punctures of the under side shallow sparse and irregular. Length, 5.4 mm.; width, 2.8 mm.

Described from Florida. One specimen, March 6, beneath decaying water hyacinth on southeast shore of Lake Okeechobee.

Cœlambus marginipennis Blatchley

Short, rounded oval, subdepressed above, moderately convex beneath. Head, thorax, femora, and tibiæ reddish brown. Elytra piceous black, shining, with narrow

side margins generally broadening into a rounded lobe at the middle. Tarsi and apical fourth of antennæ dusky. Clypeus broadly rounded, distinctly margined. Head and thorax finely, evenly, but not densely punctate; elytra more coarsely and densely punctate. Meso- and metasterna coarsely, rather sparsely and deeply punctate; abdominal punctures finer and more shallow. Length, 3.5–3.8 mm.

Sarasota, frequent in shallow, brackish pools, March (Blatchley); Punta Gorda, November (Lutz, Davis, and Leng). Belleair, January to March, and Biscayne Bay (Slosson Coll.); Sarasota, March, and Jacksonville, August (Roberts Coll.). Described from Florida.

***Hydroporus cimicoides* Sharp**

Elongate oval, slightly attenuate behind. Densely pubescent, somewhat opaque, densely and distinctly punctate. Head and thorax fuscous, with testaceous markings; antennæ fuscous, base testaceous. Thorax broadly margined. Elytra fuscous with somewhat indistinct testaceous markings; epipleuræ carinate. Body, beneath, and legs fuscous. Length, 5.5 mm.; width, 2.65 mm.

Lake Harney, one specimen in U. S. N. M., and Port Orange, one specimen in Leconte Collection (Sherman); Enterprise, April, in lake shore debris (Brownell in Leng Coll.).

This is one of the few species of *Hydroporus* which seems to be at home in the Southeastern States, occurring in Florida, South Carolina (Beaufort), near Richmond, Virginia, and at Lakehurst, N. J. The original description merely gives North America as the locality.

***Hydroporus undulatus* Say**

Oval, slightly attenuate behind. Head reddish yellow, somewhat finely and moderately punctate. Thorax reddish yellow more or less intermixed with fuscous, pubescent, more coarsely and closely punctate than the head. Elytra blackish, with more or less distinct irregular reddish brown markings; punctation and pubescence similar to that on the thorax. Under side reddish brown, somewhat densely and coarsely punctate; central portion of the metasternum, the internal plate of hind coxæ and ventral segments somewhat sparsely but very noticeably pubescent. Legs of same color as the under side. Length, 4–4.5 mm.

Common (Schwarz); Sanford, March (Blatchley); Fort Myers, April, at light (Davis); Monticello, October, and Gainesville, September and October (Mutchler and Watson).

It is well known that we have several undescribed species of *Hydroporus* related to Say's *undulatus*, and it is not altogether certain what species is entitled to this name. The species described above is a characteristic

Floridian form. Say, in the original description, says that the specimens from which his description was made were found in a pond near Bowyer Creek, Upper Missouri, and it is not uncommon in Pennsylvania.

***Hydroporus republicanus* Sharp**

Oval, rather convex, slightly elongate. Ferrugineous above, more or less infusate. Prothorax slightly margined. Posterior coxæ strongly, closely but not densely punctate. Length, 4 mm.; width 2.12 mm.

St. Augustine (Schwarz, citing C. W. Johnson's collecting and Dr. Hamilton's identification). The original description merely cites North America as the locality.

The paucity of species of *Hydroporus*, a genus enormously developed in the more northern States, is a striking feature of the Floridian aquatic fauna, paralleled by the scarcity of many northern genera of Carabidæ. No West Indian *Hydroporus* are known to us.

It is most likely, judging from the results of Prof. Bradley's collecting in the Okefinokee region of Georgia, that some of the species of *Hydroporus*, found in running water, will eventually turn up in northern Florida.

***Celina angustata* Aubé**

Elongate. Brownish red, shining. Thorax finely and sparsely punctate. Elytra darker than thorax; somewhat finely and not densely punctate; disk with a line of coarser punctures and a few others scattered over the surface; apices acuminate. Under side finely and sparsely punctate, reddish brown; legs of same color. Length, 4.0–4.5 mm.

Fort Capron, Enterprise, Jacksonville, St. Augustine, and Biscayne Bay (Schwarz); Florida (Brownell in Leng Coll.). Occurs in Southern States, not common. Aubé, in his description, says the species is found in North America and Cayenne.

***Celina slossoni*, new species**

Elongate, parallel. Head reddish brown, with piceous markings; finely and sparsely punctate; and with a pair of impressions on the front between the eyes. Thorax reddish brown, marked with piceous along the base and apex, sparsely and finely punctate but with a row of coarse punctures at the apex and another at the base separated at the disk. Elytra piceous, outer margins slightly reddish brown; more coarsely punctate than the thorax; an indistinct groove on the disk extending from near the base and becoming obliterated at the apex; apices acuminate and

with a few long scattered fulvous hairs. Under side reddish brown, somewhat shining; hind coxal plate coarsely punctured on the outer two-thirds, nearly impunctate towards the inner margin; first ventral segment somewhat alutaceous; third, fourth, and fifth segments with a slightly punctured, more or less pubescent, impression about the middle; last segment with a few long hairs; otherwise, the ventral part is very finely and sparsely punctate and slightly alutaceous. Legs of same color as under side; femur somewhat alutaceous; middle tibia of male slightly curved and narrowed at middle, basal portion somewhat slender, apical much broader; front and middle tarsi with the last joints nearly as long as the three preceding together; hind tarsi with the first joint subequal in length to the next two combined; last joint, including claws, as long as the first. Length, 4.5–5.5 mm.; width, 1.75–2. mm.

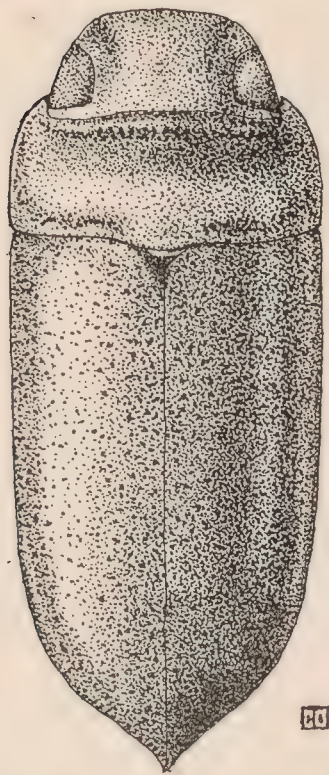


Fig. 2. *Celina slossoni*
Mutchler.

Holotype (male), No. 24286; allotype, No. 24287; and paratypes, Nos. 24288 and 24289 — The American Museum of Natural History — all from Sanford, Florida, February, except one paratype from Lake Worth, Florida. There are also two specimens from Enterprise, December, in the Leng Collection and nineteen specimens from Sanford in the Sherman Collection.

Slossoni approaches *grossula* in size and resembles it also in being generally rather dark. It differs not only in the transverse blackish bands at front and hind margins of thorax but also in the punctuation of the upper surface, which is sparser in *slossoni* than in *grossula*, particularly on the disk of the thorax.

Dedicated to Mrs. Annie Trumbull Slosson, in grateful recognition of her many additions to the list of Floridian beetles and of her constant kindness to us.

***Celina grossula* Leconte**

Chocolate brown, shining. Head and thorax paler, finely and not densely punctate; thorax with a row of larger punctures at base of apex; elytral punctures slightly coarser and more dense, with three indistinct lines seemingly formed by slightly larger punctures, the first at the suture, the second on the disk, and the third at the margin. Apices of elytra slightly acuminate. Under side finely and sparsely punctate. Length, 5 mm.

Enterprise and Jacksonville (Schwarz); Everglade, May (Davis); Sanford, July, and Marion Co. (Sherman). Described from Louisiana. Occurs also in Cuba.

COLYMBETINI

***Copelatus chevrolati* Aubé**

Elongate, oval, subdepressed. Head and thorax reddish brown, lighter at the margins. Thorax with a row of punctures at the sides. Elytra reddish brown, sides slightly paler, each with eight striæ; also a short stria at the apex between the margin and first stria and a line of punctures near the margin. Under side fusco-piceous, but legs somewhat paler. Length, 6 mm.; width, 3.25 mm.

Fort Capron and Tampa, rare (Schwarz); Taylor Co. and Hastings (Genung in Sherman Coll.); Enterprise, December (Leng Coll.); Dunedin, January to March (Blatchley); Jacksonville, June, and Taylor Co., July (Roberts Coll.). Crotch gave a wide distribution for this species, including Lake Superior, Kansas, Texas, Arizona, and California. No specific locality is mentioned in the original description.

***Copelatus glyphicus* (Say)**

Oblong-ovate, rather narrow, subdepressed. Dark reddish brown or piceous, but antennæ and legs paler. Thorax nearly smooth. Each elytron with ten deeply impressed striæ, reaching scarcely to the apex. Body, beneath, sparsely strigose. Length, 5-6 mm.

St. Augustine and Lake Worth, common (Schwarz); Arch Creek, March (Blatchley); Lakeland, November (Lutz, Davis, and Leng); Enterprise, November (Leng Coll.). Say, in the original description, mentions that he found it in numbers in fresh water ponds on Sullivan's Island, South Carolina, also that it is listed in Melsheimer's Catalogue. Vermont to Pennsylvania (Roberts Coll.). Crotch gave Lake Superior, Kansas, Texas, Louisiana, and Florida. Occurs also in Cuba and Guadeloupe.

***Copelatus cælatipennis* Aubé**

Oval, subdepressed. Head, thorax, elytra at base and sides, antennæ, and legs rufous. Thorax minutely strigate, the strigæ continued almost to apex, marginal one longest. Each elytron with ten striæ. Body, beneath, reddish; abdomen darker. Length, 4.5 mm.; width, 2.25 mm.

Sanford, Jacksonville, and Taylor Co. (Sherman Coll.); Lakeland, November (Lutz, Davis, and Leng); Taylor Co., July, Sanford, and Jacksonville, August (Roberts Coll.). Described from the Antilles.

In studying *Copelatus*, reference should be made to Schæffer, Journ. N. Y. Ent. Soc., XVI, 1908, pp. 16-18.

Matus bicarinatus (Say)

Elongate oval, slightly convex. Uniform brownish red, shining, but antennæ paler. Thorax rounded at the sides, front angles acute. Elytra each with two or three rows of faint dorsal punctures. Length, 8–9 mm.

Included in Hubbard and Schwarz list but unseen by them. Arch Creek, March (Blatchley); Lake Okeechobee, one specimen, April 30 (Grossbeck); Taylor Co.? (Roberts Coll.). Mr. Sherman was at first disposed to question the occurrence of this northern species in Florida, but accumulated evidence shows it to be present, although rare. Mr. Loding finds it in Alabama. The original description makes no mention of the type locality.

Coptotomus interrogatus var. **obscurus** Sharp

Elongate oval, convex; shining. Head, thorax, and antennæ reddish yellow, the outer antennal joints being slightly darker and the thorax with middle of apex and base pitchy brown; finely and closely punctate. Elytra pitchy brown; with reddish yellow markings consisting of a short stripe on each side near the scutellum, and a marginal one recurved at the humerus and becoming somewhat broken on the apical third. Under side reddish brown. Length, 7 mm.; width, 3.75 mm.

St. Augustine, common (Schwarz); Enterprise, November (Leng Coll.); Monticello, October (Mutchler and Watson); Sanford, August, Enterprise, and Jacksonville, July (Roberts Coll.); Lake Worth and Atlantic Beach, January to March (Slosson Coll.); Arch Creek and Dunedin, January and March (Blatchley); Econ. River,¹ March (Brownell in Leng Coll.); Jacksonville, April 21 (Laurent). This last record displaces that of *Agabus* n. sp. (Ent. News, 1879, p. 7), the specimens having since been identified by Mr. Sherman at Mr. Laurent's request. So far, no species of *Agabus* is known to occur in Florida. *C. interrogatus* was described from Massachusetts, and *obscurus* from Texas and Florida. The southern forms seem to show a varietal difference from the northern ones. Sharp says that *obscurus* is excessively similar to *interrogatus* Fabricius and *longulus* Leconte but is smaller and darker in color, especially beneath, and has the hind coxæ more free from sculpture and their front border nearer to the middle coxal cavities. The sexual distinctions are also less conspicuous. Crotch gave the distribution of *interrogatus* as Pennsylvania, Georgia, Texas, Missouri, and California.

¹ It is impossible to say whether this abbreviation refers to the Econfina River in Washington County or the Econfino River in Taylor County, but we believe that the latter is the locality referred to.

Rhantus calidus (Fabricius)

Ovate, subconvex. Black, slightly shining. Head (at vertex) and thorax (at apex and sides) reddish yellow. Elytra with a subbasal transverse line, three narrow vittæ, and lateral margin pale reddish yellow; also numerous small spots, more dense between the second and third vittæ and at apex, of the same color. Antennæ, under side, and four anterior legs rufous; posterior legs slightly darker. Male with tarsal claws of middle leg equal. Length, 12.5–13.5 mm.

Buck Key (Schwarz); Lake Worth and Belleair, January to March (Slosson Coll.); Sarasota, March (Blatchley); Lakeland, November, in a grassy pool (Davis); Enterprise, November (Brownell in Leng Coll.); Taylor Co., July, and Jacksonville, August (Roberts Coll.). Crotch recorded it from Georgia. Described from South America. It is known from Cuba, Haiti and Guadeloupe.

Hydaticus bimarginatus (Say)

Oval, moderately convex. Head and thorax reddish; basal margin of head darker. Thorax at base with a dark line dilated at the middle. Elytra uniform piceous with a submarginal yellow stripe recurved at the humerus, the apical portion often broken and not reaching the apex. Antennæ, palpi, and four front legs yellowish; hind legs darker. Ventral segments dark, with obsolete lighter submarginal spots. Length, 11.5–12 mm.

Fort Capron, Tampa, and Jacksonville (Schwarz); Lake Worth, January to March (Slosson Coll.); Enterprise, September and October (Brownell in Leng Coll.); Tampa, August (Bradley); Titusville, November (Lutz); Clearwater, April, and Sanford, May (Van Duzee); Taylor Co., July, and Jacksonville, July and August (Roberts Coll.). Crotch gave Pennsylvania, Georgia, Florida, and Louisiana. Described from Louisiana. The genus is represented in the West Indies by two allied species, *cinctipennis* and *rimosus* of Aubé.

Thermonectes basilaris (Harris)

Ovate, subconvex. Above black. Head in front and a transverse line on the vertex dull yellow. Thorax with a discal line and sides broadly dull yellow. Elytra at margins and a subbasal transverse line and some ill-defined markings at the sides and apical part yellowish. Antennæ and front legs testaceous; hind legs and under surface reddish brown or piceous. Length, 11.5–13 mm.

Fort Capron, Lake Ashby, Tampa, Jacksonville, St. Augustine, Lake Worth, and Buck Key (Schwarz); Arch Creek, March (Blatchley); Day-

tona, November (Engelhardt); Lake City, June (J. R. Watson); Lakeland, November, in a grassy pool (Davis); Sanford, May (Van Duzee); Lake Okeechobee, April, Punta Gorda, Jacksonville, and Titusville, November (Amer. Mus. Coll.); Jacksonville, June, and Sanford (Roberts Coll.). Crotch gave Canada, Pennsylvania, Georgia, and Texas. This species is known from Cuba and Guadeloupe.

Variety *ornaticollis* (Aubé) is dull yellow above. Head with vertex and an M-shaped mark black. Thorax with two transverse black lines. Elytra punctate as in the above. Length, 11.5–13 mm. Under the name *basilaris* var. from Lake Worth (Slosson Coll.); Key West (?) (Angell Coll.); Jacksonville, August (Roberts Coll.). Described from Mexico and the United States. Crotch gave the distribution as Pennsylvania, Illinois, and Kansas.

Thermonectes latecinctus (Leconte). There are specimens bearing this name in the Slosson Coll. from Lake Worth, January to March; also others collected at Enterprise by Brownell in the Leng Coll. However, the name rightly applies to southwestern forms. The original description citing the locality as “ad flumen Colorado et Vallecitas.”

CYBISTRINI

Cybister fimbriolatus (Say)

Ovate, more or less wedge shaped. Above brown with a greenish tinge. Thorax and elytra with a broad yellow margin. Front of head, four front legs, and spots at sides of ventral segments 3–6, yellow. Thorax and elytra of female finely strigose; suture more or less smooth. Stridulating plate of male with four distinct ridges. Length, 30–33 mm.

Jacksonville, January to March, and Biscayne Bay (Slosson Coll.); Jacksonville (Ashmead); Jacksonville (Castle and Laurent); Daytona, November (Engelhardt); Lake City, March and June (J. R. Watson); Fort Myers, April, at light (Davis). Crotch gave the distribution as Pennsylvania, Georgia, Kansas, and Louisiana. No specimens from Florida in the Roberts Collection. Described from Pennsylvania.

Cybister olivieri Crotch

Similar to *fimbriolatus* but with the thoracic and elytral margins narrower; the yellow marginal stripe leaves the margin behind the middle and ends in an attenuate point. The male stridulating plate has only three distinct ridges. Length, 28–32 mm.

New Smyrna, Tampa, Cedar Keys, Jacksonville, St. Augustine, and Lake Worth (Schwarz); Jacksonville (Leng Coll.); Hillsboro Co., Marion Co., and Jacksonville (Roberts Coll.). Described from Florida. The genus *Cybister* is represented in Cuba by the species *occidentalis* Aubé.

Megadytes fraternus Sharp

Broadly oval, subconvex, narrowed anteriorly. Head, front, and sides of thorax, testaceous. Elytra near the apex spotted with ferrugineous. Under side black; four anterior legs rufous; middle tarsi piceous; posterior legs piceous black. Antennæ very slender, testaceous. Elytra of female thickly sculptured with very short, but regular, linear impressions, which cover the surface except for a small space on the extreme apical portion. Length, 22.5 mm.

West Palm Beach, June (Dury). A West Indian species known from Antigua, Guadeloupe, Haiti, Porto Rico, for which this is the first Floridian record. The species was described by Sharp from specimens found in Panama, Guatemala, Guadeloupe, St. Domingo, and Demerara.

The following West Indian Dytiscidæ are not even generically represented in Florida:

Eunectes sticticus (Linné).—Guadeloupe, St. Bartholomew, Central America, Arizona, Lower California, etc.

Derovatellus lentus (Wehncke).—Central America and Porto Rico.

Suphis cimicoides Aubé.—Guadeloupe.

Pachydrus.—Five species; Antigua, Guadeloupe, Porto Rico, and Cuba.

Pronoterus obscuripennis Fleutiaux.—Guadeloupe.

These are nearly all confined to the Lesser Antilles, and, excluding them, it may be said that the family is represented in Florida and the Greater Antilles by the same genera and to a considerable extent by the same species; seven Floridian species out of forty-two are absolutely identical, and several others are at least closely allied. Taxonomically, *Pachydrus* is closely related to *Bidessus* and *Desmopachria*; *Suphis* is closely related to *Colpius*; but *Pronoterus* is tribally separated and *Derovatellus* is of subfamily separation according to Dr. Sharp's arrangement. That is, the greater the taxonomic separation the lesser the representation in the Greater Antilles, indicating, as we have already seen in the Carabidæ, a strong bond between the Floridian and Cuban fauna. There is a similar bond (though a much weaker one) between the South American fauna and that of Lesser Antilles.

As intimated above, the remaining families of water beetles are not surely adephagous, though the Haliplidæ have usually been associated, in

systems of classification, with Carabidæ and Dytiscidæ. Sharp and Muir, after a year's study of the genitalia, keep the Haliplidæ in Adephaga but find "their differentiation from the Byrrhoid type [which includes Gyrinidæ, Hydrophilidæ and Parnidæ] is not great." Of Gyrinidæ, they speak more strongly: "The structure of Gyrinidæ is on a different plan from that of the Caraboidea. When it is remembered in addition to this that all the members of this family are highly specialized for a mode of life that is shared by no other Coleoptera, we are justified in concluding that this has always been an isolated family." "They should not be placed with the Dytiscidæ but near the Hydrophilidæ." These remarks are quoted from the paper by Sharp and Muir (Trans. Ent. Soc. Lond., 1912) on the 'Comparative Anatomy of the Male Genital Tube in Coleoptera.' The families Gyrinidæ, Hydrophilidæ, and Parnidæ are placed in the first, or Byrrhoidea, division — under which name they include twenty or thirty other families, the Byrrhidæ being treated on the whole as the most central of the families. Their conclusion concerning the phylogenetic rank is summarized as follows: "The complex is of considerable importance, as it is possible to consider that we are here in the presence of the more primitive of the conditions of the coleopterous genital tube, so far as existing forms are concerned. We use this qualification because the structures are very far from being truly primitive."

HALIPLIDÆ

These insects are found in still water in which there is a growth of filamentous algæ, for clinging to which the claws of these insects are specially adapted. In this family the descriptions of Matheson (Jour. N. Y. Ent. Soc., XX, 1912) and Roberts (*op. cit.*, XXI, 1913) were made without mutual comparison of material, and it becomes necessary to combine their contributions and add that of Blatchley ('Beetles of Indiana,' 1910) in order to review the Floridian fauna. To facilitate the identification of the reader's specimens, we have prepared the following key to the species involved, adding two species, *Haliphus lewisii* and *Peltodytes pedunculatus*, which have been reported but which we believe are now covered by more recent names.

Key to Haliplid Genera of Florida

- A.—Terminal joint of palpi small, subulate, shorter than the preceding; posterior coxæ concealing only the first three segments of abdomen.....*Haliphus*.
 AA.—Terminal joint of palpi large, conical, longer than the preceding; posterior coxæ concealing all but the last segment of abdomen.....*Peltodytes*.

Haliphus

The Floridian species all have the pronotum without paired basal impressions (present in *ruficollis* which is common over the region north of Florida); prosternum distinctly margined; black markings always present. They are distinguished as follows:

1. Small species (2.0–3.0 mm.); pronotum immaculate or with a piceous patch wider at hind margin.....2.
Larger species (3.75–4.50 mm.); pronotum with a round black spot at middle of front margin; elytra with six black spots more or less confluent; punctures large and deep.....*punctatus*.
2. Pronotum immaculate; smaller (2.0–2.5 mm.).....3.
Pronotum with piceous patch; elytra with confluent piceous patches leaving only small spots of the ferrugineous ground color; 3.0 mm.....*havaniensis*.
3. Elytra with black bands on base, across middle, and at apex, extending nearly across elytron, the middle one more irregular in outline; apices not denticulate; 2.0–2.5 mm.....*annulatus*.
Elytral maculation indistinct; apices slightly denticulate; 2.5 mm. (Not Floridian; included for comparison only).....*lewisii*.

Haliphus punctatus Aubé

Lake Harney and Cedar Keys, not rare (Hubbard and Schwarz); Sebastian River (Schwarz Mss. notes); Jacksonville, August, and Sanford, February and July (Roberts Coll.); Middle and Southern States (Crotch); Florida, Texas, and Louisiana (Roberts Coll.). The specimens on which the Crotch record of "Middle States" is based (quoted also by Matheson) are excluded by Roberts and the species, as restricted, is confined to the Gulf Strip. The original description merely gives the United States as the locality.

Haliphus havaniensis Wehncke (*confluentus* Roberts)

Originally described by Wehncke (Entom. Zeit. Stettin, XLI, 1880, p. 74) from Cuba; redescribed by Roberts (Journ. N. Y. Ent. Society, XXI, 1913, p. 106) as *confluentus*; and apparently unknown to Matheson, who gives no definite Floridian citations for any species of *Haliphus*. Taylor Co., Sanford, and Jacksonville (Genung), and Tampa (U. S. Nat. Mus.) are the localities cited by Roberts, whose types are now in this Museum and show his species to be identical with the Cuban one. The Taylor County and Jacksonville specimens are labelled July.

Haliphus annulatus Roberts

Described from Florida in 1913; the types from Taylor Co., July (Genung) are now in this Museum. Also Jacksonville, August (Roberts Coll.); Titusville, Nov. 8, in a roadside pool (Lutz). With this we combine the records for *H. lewisii*, a species reported from Texas (Roberts), Indiana and Wisconsin (Matheson), believing that all Floridian specimens are covered by the *annulatus* description. These are Lake Worth (Slosson Coll.) and Florida (Blatchley). Roberts gave the range as Florida and South Carolina.

Peltodytes

1. Posterior femora entirely black or brown.....2.
Posterior femora more or less pale.....(Allied northern species).
2. Elytra with a subhumeral spot or dash of black.....3.
Elytra without subhumeral spot or dash of black; median spots coalescent on suture, forming a black blotch; 3.5-4 mm.....*muticus*.
3. Last abdominal segment shining, polished.....4.
Last abdominal segment dull, rugose; spots large, distinct, the median coalescent with the sutural margin; coarse punctures of elytra extending beyond the middle of elytra; 3.5-4 mm.....*oppositus*.
4. Spots smaller, distinct, the median barely touching sutural margin; 3.5 mm.
(Not yet found in Florida).....*pedunculatus*.
Spots larger, confluent, the median distinctly coalescent with the sutural margin; coarse punctures of elytra extending to middle; 3.5 mm.....*floridensis*.

Peltodytes oppositus Roberts

Described from Florida; types in this Museum. Jacksonville (Genung), November, (Lutz, Davis, and Leng); Fort Myers, November, found in almost still water.

Peltodytes floridensis Matheson

Described from Sanford, Florida.

Peltodytes muticus (Leconte)

Crescent City and St. Augustine (Schwarz); Sanford (Roberts and Matheson). The *Cnemidotus 12-punctatus* of the Hubbard and Schwarz list, which occurs in more northern regions and differs from all Floridian

species by its partly yellow femora, is probably covered by this name. Described from the Middle and Western States.

There have been three species of Haliplidæ described from the West Indies and the family is known from Cuba, Haiti, Guadeloupe, and Antigua.

GYRINIDÆ.

These are the whirligig beetles. They are common during the day on the surface of the water, where they congregate in restless groups.

Dineutes

Key to the Floridian species

1. Sutural angles of elytra rounded in both sexes.....2.
Sutural angles of elytra distinct, frequently produced, in both sexes.....3.
2. Femora of male with a strong acute tooth; sutural angles of elytra broadly rounded, apices not serrate. Length, 10–11 mm.; width, 6–7 mm.
emarginatus.
- Femora of male with a weak tooth, scarcely more than a termination of the ridge on the under side; sutural angles of elytra scarcely rounded, apices very finely serrulate. Length, 9–10 mm.; width, 5.5–6 mm.....*carolinus.*
3. Under surface brown or testaceous; femora of male toothed.....4.
Under surface black, more or less tinged with brown, shining; anterior tibiæ regularly broadened from base to apex, exterior angle rectangular; middle and hind legs testaceous; femora of male not toothed. Length, 10–11 mm.; width, 5.5–6 mm.....*assimilis.*
4. Apices of elytra serrulate.....5.
Apices of elytra not serrulate. Size small; narrow, very convex. Upper surface polished black; under surface and legs rufous. Tooth on femora of male minute. Length, 9–10.5 mm.; width, 4.5–5.5 mm.....*angustus.*
5. Size medium to small. Upper surface very highly polished, not bronzed; under surface chestnut brown, shining; serration of elytra distinct. Length, 9–12 mm.; width, 6–6.5 mm.....*serrulatus.*
Size medium. Upper surface not highly polished, bronzed; under surface pitchy brown; serration of elytra fine. Length, 11–11.5 mm.; width, 6–6.5 mm..... *analis.*

Dineutes analis Regimbart

Biscayne Bay and Atlantic Beach, January to March (Slosson Coll.). Described from Louisiana and Texas. Roberts gave Texas as the habitat.

Dineutes emarginatus (Say)

Florida (Blatchley). No type locality is given in the original description, but Roberts gave Northern and Middle Atlantic States, south to Virginia, as the distribution.

Dineutes carolinus Leconte

Fort Capron and Sand Point, not rare (Schwarz); Buck Key (Schwarz); Lake City, April (J. R. Watson); Lake Parker, near Lakeland, November (Davis); Deep Lake and Lake Okeechobee, April (Grossbeck); Everglade, May and July, and Fort Myers, April, at light (Davis); Monticello and Pensacola, October (Mutchler and Watson); Dunedin, March, and Ormond, April (Blatchley); Sanford, February (Roberts Coll.). Described from South Carolina. Roberts gave South Atlantic States, Louisiana, and Texas as the habitat.

Dineutes serrulatus Leconte

Sand Point, Enterprise, Lake Ashby, and St. Augustine (Schwarz); Florida (Blatchley); Crescent City and Deep Lake, April (Grossbeck); Gainesville, September and October (Mutchler and Watson); Enterprise, June, and Kissimmee and Orange Co., April (Roberts Coll.); Levy Co. (Laurent). Described from the Middle and Southern States, but Roberts gave Florida only for all the specimens which he saw of this species.

Dineutes angustus Leconte

Described from Florida; recorded also from Virginia by Roberts. No Floridian specimens in Roberts' Coll.

Dineutes assimilis Aubé

St. Augustine (Schwarz). The original description merely gives the United States, but Roberts gave a wide distribution: Northern, Middle and Southern Atlantic States, also New Mexico, Colorado, Minnesota, Michigan, and Dakota; there are no specimens from Florida in his collection.

Gyrinus

Key to the Floridian species

1. Scutellum finely but distinctly carinate; upper surface not polished.....2.
Scutellum flat; upper surface polished.....3.
2. Under surface always ferruginous yellow; inflexed margins and legs ferruginous;
3.5–4.5 mm.....*minutus*.
3. Epipleuræ metallic black, rarely with a feeble rufous tinge.....4.
Epipleuræ and under side of margin of thorax testaceous; above black, highly
polished, broadly bronzed on the sides; tips of elytra truncate, slightly rounded,
outer angle not very distinct; under side rufo-ferruginous; mesosternum and
posterior coxæ (especially in the female) frequently piceous; 5–5.25 mm.
elevatus.
4. Upper surface highly polished.....5.
Upper surface not highly polished; black bronzed above and beneath; elytra
with tips broadly rounded; outer rows of punctures but little stronger than
inner ones; legs and last ventral segment ferruginous; 5–6 mm. (Not re-
corded from Florida)..... *analis*.
5. Upper surface black shining; margins and sides bronzed; elytra with rows of
deeply impressed bronzed, coarse punctures, so approximated that the outer
striae seem impressed; 5.25–5.75 mm.....*parcus*.
Upper surface black, highly polished, with bluish reflections; margins and sides
bronzed; elytra with rows of punctures which are not closely approximate,
outer rows a little stronger, not impressed; 6 mm.....*pernitidus*.

Gyrinus elevatus Leconte

Common (Schwarz); St. Augustine (C. W. Johnson); Gulf Hammock (Castle and Laurent); Florida (Engelhardt); Lake City, April (J. R. Watson); Lake Okeechobee, April and May (Davis and Grossbeck); Lake City, April (Leng Coll.); Dunedin, February (Blatchley); Orange Co. (Roberts Coll.). Described from New York.

Gyrinus pernitidus Leconte

Monticello, October (Mutchler and Watson). No type locality is given.

Gyrinus minutus Fabricius

Gulf Hammock (Castle and Laurent); Gainesville, October (Mutchler and Watson). An abundant species at Lake Superior. Under the name *rockinghamensis* Leconte (treated as a synonym in the 'Catalogus'), Jack-

sonville (Ashmead); Econ. River, March (Brownell in Leng Coll.); noted as unseen in Hubbard and Schwarz List. Sanford, February, and Enterprise, March (Roberts Coll.). Described from North Carolina.

Gyrinus parvus Say

Florida (Roberts Coll.). Described from Mexico.

An unnamed species is noted from Biscayne Bay in Schwarz Mss. notes. It may be one of the following, for which southern distribution is indicated by Leconte: *analis*, Lake Superior to North Carolina, and *parvus*, Tex.

In the West Indies, a few species of *Dineutes*, *Gyrinus*, and *Gyretes* are known, but as yet there is no known instance of actual specific identity.

HYDROPHILIDÆ

The Hydrophilidæ are regarded as being phytophagus. Some are powerful swimmers, but the first three genera belong to a group possessing but feeble natatorial powers.

HELOPHORINI

Hydrochus

Very little work has been done on the species of this genus for a number of years, probably not only from a lack of material but also from the extreme difficulty in separating the species and in recognizing the described species without comparison with the types. There are four species which have surely been credited with occurring in Florida; they are as follows:

H. rugosus, 6 mm. in length, is the largest species. Color, gray with a coppery reflection. Thorax trapezoidal, not longer than wide; dorsal foveæ slightly impressed, the three anterior larger. Elytra striate punctate; interstices on posterior part elevated forming small callosities. Beneath, black. Tibiæ and tarsi, red.

The next in size, *H. foveatus*, is 3.5 mm. in length. Color, shining gray. Thorax slightly longer than wide, slightly angustate posteriorly, sides nearly straight; dorsal foveæ large and deep, two basal ones smaller. Elytra punctate-striate; posterior part with callosities; suture and alternate interstices elevated; third and fifth interstices interrupted at posterior part, fourth with its posterior part elevated.

H. inæqualis, 3 mm. in length, is dark reddish brown, slightly bronzed. Thorax slightly longer than wide; sides subsinuate, finely crenulate; dorsal foveæ distinct. Elytra punctate striate; the fifth, seventh, and ninth interstices elevated and in-

interrupted behind the middle, giving the appearance of a transverse impression; fourth elevation opposite the break in the third. Legs red.

The smallest species recorded, *H. simplex*, 2.5 mm. in length, is black with a bronze reflection. Thorax slightly angustate posteriorly; sides slightly crenulate; dorsum with the two basal foveæ more marked. Elytral striæ of the same width as interstices. Legs rufo-testaceous.

There are also four species which either may be found in Florida or whose names have been attached to Floridian specimens:

The largest of these, *H. scabratus*, 5.5 mm. in length, is slightly darker than *rugosus* but without coppery reflection. The elytral striæ are less impressed and the interstices have large tubercular elevations, giving the insect a scabrous appearance. Described from Middle and Southern States.

H. excavatus, 3.5–3.9 mm., is related to *inæqualis* but of darker color and the interruptions of the elytral striæ are less apparent; the fifth interstice is elevated about the middle and interrupted; adjacent to this interruption the fourth and seventh are slightly elevated. Described from Louisiana and cited by Hubbard and Schwarz.

H. rufipes, 3.25 mm., is related to the preceding, but the thorax is less narrowed behind and the interstices of the elytra are distinctly wider than the striæ. Described from Middle and Southern States.

H. variolatus, 3.25 mm., described from San Diego, is very questionably found in Florida. It is dark gray with metallic reflection. Thorax slightly longer than wide; sides crenulate; dorsal foveæ moderately deep. Surface of the elytra not perceptibly uneven, except for the slight posterior elevation of the fifth interstice. Legs testaceous; basal joints of femora darker. This name has been applied to specimens from Biscayne Bay and Lake Worth in the Slosson collection.

Hydrochus simplex Leconte

Belleair and Biscayne Bay, January to March (Slosson Coll.); Punta Gorda and Titusville, November (Lutz, Davis, and Leng). Described from Louisiana.

Hydrochus rugosus Mulsant

Enterprise and Tampa, rare (Hubbard and Schwarz); Belleair (Leng Coll. received from Mrs. Slosson); Monticello, October (Mutchler and Watson). The original description merely gives North America but Leconte gave Middle States for this species and described *callosus*, which is regarded as synonymous, from Louisiana. Cuban specimens have been identified as this species by Mr. Wintersteiner.

Hydrochus inæqualis Leconte

Common (Hubbard and Schwarz); St. Augustine (Schwarz Mss. notes). Described from Louisiana.

Hydrochus foveatus Haldeman

Monticello, October (Mutchler and Watson), identified by Mr. F. Wintersteiner. Described from Texas.

Three species are known from Cuba, one of which appears to be identical with *rugosus*, cited above. Two species are known from Porto Rico.

Ochthebius attritus Leconte

Piceo-testaceous; surface aeneous; legs pale. Thorax gradually, sinuately narrowed from apex to base; transparent border narrow, continuing the curve of the anterior third; discal fovea shallow or nearly absent; lateral impression deeper and more coarsely punctured; median line distinct, extending about two-thirds the length of thorax. Elytral striae scarcely impressed; punctures closely placed and subquadrate; lateral margin spread out and flattened from humerus to beyond middle, but not reaching the apex. Length, 1.5 mm.

Including *simplex* Leconte as a synonym, Haulover, on the lagoon beach (Hubbard and Schwarz). Described from Florida.

Ochthebius foveicollis Leconte

Piceous; surface aeneous; legs pale. Thorax abruptly arcuately narrowed from one-fourth behind the apex; a second sinuation behind the middle; transparent border broad, gradually arcuate; discal fovea moderately deep and well separated; lateral impressions large and deep; median line long and deep. Elytra with striae of closely placed punctures; margin of transparent border continuous. Length, 1.2–2.5 mm.

Lake Harney and Enterprise, not rare (Hubbard and Schwarz); Enterprise, June (Roberts Coll.); Titusville, November 8, in a grassy ditch beside railroad track (Lutz). Described from Lake Harney. Dr. Horn's revision of the genus gives a wide distribution: Pennsylvania, New Mexico, and Florida. We have, so far, no West Indian records for any definite species, but the U. S. Nat. Museum has examples of the genus from Cuba and Porto Rico.

Hydræna marginicollis Kiesenwetter

Surface shining. Head black, somewhat coarsely and closely punctate. Thorax black; with anterior and posterior margins testaceous; somewhat coarsely and closely punctate; with a broad fovea on each side before the middle. Elytra piceo-testaceous, ornamented with rows of moderately coarse, closely placed punctures. Under side black. Legs and palpi, testaceous. Length, 1.25 mm.

Rare (Hubbard and Schwarz); Punta Gorda, November (Lutz, Davis, and Leng); Enterprise, November and December, in lake shore debris (Brownell). Leconte recorded it from New Orleans. According to the original description this species was found in New Orleans, Louisiana, and in the West Indies; this last record was overlooked by the authors in their list of Coleoptera of the West Indies and the species should be added to that list (See Linnæa, Entomologica, IV, 1849, pp. 177-178).

HYDROPHILINI

Tropisternus

According to records at hand, there are five species of this genus to be found in Florida, but further investigation may prove that the records for *lateralis* and *nimbatus* refer to the same species. There is also a series of three specimens in the Museum collection which was identified by Mr. F. Wintersteiner as *quadristriatus* Horn. This species was described by Dr. Horn (Trans. Amer. Ent. Soc., III, 1871, p. 331) from near the seacoast of New Jersey, but later (Trans. Amer. Ent. Soc., V, 1876, p. 252) he found it to be synonymous with *sublævis*. The only difference which we can see in the Floridian specimens is the predominating testaceous color of the legs. The following notes may be of some assistance to the student.

The separation of the species of this genus into groups is based upon the shape of the prosternal groove, whether open or closed in front. The species *striolatus* (9-10.5 mm. in length) has the groove open; thorax and elytra coppery black margined with yellow, the latter with yellow stripes on the disk; under surface black with prosternum and legs brownish yellow. The other four species from Florida have the prosternal groove closed in front. Two of these, *nimbatus* and *lateralis*, are of equal length, 8.2-9 mm. The thorax and elytra are olivaceous black, margined with pale yellow. Under surface black or piceous; legs yellow; base of femora black. Those with a narrow marginal stripe are referred to as *nimbatus* and the ones with a broader stripe as *lateralis*. The other two have the thorax and elytra uniformly black above. Of these, *sublævis* is 9-10 mm. in length, elongate oval with minute indistinct punctures on the elytra. Antennæ, palpi, and legs dull yellow; base of femora piceous. Front half of sternal crest flat, finely but distinctly punctured. The other, *glaber*, is 9.5-11 mm. in length, is more broadly oval. Elytral punctures slightly larger and more distinct. Palpi flavous, apex of last joint brown. Legs black, more or less variegated with testaceous. Front part of sternal crest concave and very coarsely punctured.

The following list of localities is probably far from complete.

Tropisternus lateralis (Fabricius)

Common (Hubbard and Schwarz); St. Augustine (Schwarz Mss. notes). Leconte gives the distribution as New York, Georgia, Nebraska, and Texas. Neither in the Roberts Collection nor in Mr. Wintersteiner's identifications does this name appear, being replaced, probably, by *nimbatus*. Known in the West Indies from Cuba to Barbados.

Tropisternus nimbatus (Say)

Lake Worth, Punta Gorda, and Biscayne Bay, January to March (Slosson Coll.); Jacksonville (Castle and Laurent); Lake City, June (Florida Agric. Exp. Sta.); Lakeland, Punta Gorda, and Titusville, November (Lutz, Davis, and Leng); Fort Myers, at light, March (Davis); Lake Okeechobee, at light, April (Davis and Grossbeck); Florida (Blatchley). The records for *nimbatus* and *lateralis* are possibly confused; both of these species were described without definite localities being given.

Tropisternus sublævis (Leconte)

Everglade, April (Davis); identified by F. Wintersteiner; confused previously with *glaber*. Described from Nebraska and Georgia.

Tropisternus striolatus (Leconte)

Enterprise, not rare (Hubbard and Schwarz); Jacksonville (Castle and Laurent); Fort Myers, March and April, at light (Davis); Punta Gorda, November (Lutz, Davis, and Leng); Clearwater, April (Van Duzee); Lake Okeechobee, April (Grossbeck); Monticello, October, and Gainesville, September and October (Mutchler and Watson). Described from, and abundant in, the Southern States.

Tropisternus glaber (Herbst)

Common (Hubbard and Schwarz); St. Augustine (Johnson); Lake Worth (Hamilton); Jacksonville, January to March (Slosson Coll.); St. Augustine, November (Engelhardt); Lake City, June (J. R. Watson); Fort Myers, at light, March and April (Davis); Monticello and Gainesville, September and October (Mutchler and Watson). Dr. Leconte gave the distribution as Lake Superior to Georgia. It has also been recorded

from Haiti, and, even though its records are confused with those of *sublævis*, it is clearly a common and widely distributed species.

Hydrophilus ovalis Ziegler

Oblong-oval; above, black with a greenish tinge. Head with irregular impressed punctures. Antennæ and palpi piceous. Thorax with punctures near the anterior angles, a series on each side and a few near the anterior margin. Elytra with four series of punctures, the third abbreviated anteriorly, the fourth double; side margin finely and closely punctured. Beneath, black with traces of a rufous spot on each segment. Length, 31–33 mm.

Jacksonville (Castle and Laurent); Lake City, June (Florida Agric. Exp. Sta.); Fort Myers, at light, March and April (Davis); Florida (Blatchley); Tampa, August (Bradley). Described from Pennsylvania. The Tampa specimens are, in part, brilliantly purplish metallic and may represent *violaceonitens* Duval, described from Cuba.

Hydrocharis castus (Say)

Oblong-oval; black; finely punctate. Head with an oblique line of coarse punctures in front and a line of punctures near the eye. Antennæ and palpi, rufous. Labrum broadly emarginate; anterior edge piceous; center with two larger punctures. Thorax with a short arcuated row of punctures near the apex and a few scattered punctures on the sides. Elytra with five rows of impressed punctures, the lateral ones being approximate to the margin. Legs, except base of femora, piceous. Length, 13–15.5 mm.

Fort Capron, very rare (Hubbard and Schwarz); Jacksonville, (Castle and Laurent); Lake Worth (Hamilton); St. Augustine (Schwarz Mss. notes); Dunedin, November (Blatchley); Daytona, June (Engelhardt); Everglade, May, Fort Myers, at light, March, and Lake Okeechobee, April (Davis); Punta Gorda, Fort Myers, and Jacksonville, November (Lutz, Davis, and Leng). Abundant in Middle and Southern States. Described from Louisiana.

HYDROBIINI

Berosus

There are six species of this genus recorded from Florida, but the separation of the species is so difficult that a revision of the whole genus will be necessary before one may be sure of his identifications. Therefore, we are

unable to give any definite key for their separation, especially as to color pattern, as there are a number of specimens in our collection from Florida which agree with the description of one or another species but the color markings are quite variable. One species (*pugnax*), 5–6 mm. in length, may be told on account of its having two spines at the apex of each elytron; another (*aculeatus*), 4 mm. in length, has the elytra prolonged at the apex, this prolongation being more noticeable in the female. The remainder do not have the elytra prolonged and are more difficult to separate. Two of these are said to have one tooth at the middle of the notch in the fifth segment (a somewhat difficult character to make out in some specimens); one of these species (*peregrinus*) measures about 4 mm. in length, while the other (*exiguus*) is very much smaller, measuring only 2.5 mm. The remaining two species have two teeth at the middle of the notch on the fifth segment. They are separated as follows: *striatus*, 4–5 mm. in length, has the stria on the elytra distinctly impressed and intervals with rather coarse punctures; while *infuscatus*, 5–6 mm. in length, has the striae on the disk of the elytra replaced by rows of fine punctures and the intervals finely punctate. The following are the locality records for the species which we have been able to recognize.

***Berosus pugnax* Leconte**

Enterprise, one specimen (Hubbard and Schwarz); Jacksonville, April (Laurent); La Belle, April (Grossbeck); Lake Okeechobee, April (Davis). Described from Louisiana.

***Berosus infuscatus* Leconte**

Lake Harney and Enterprise, not rare (Hubbard and Schwarz); Lakeland, Jacksonville, and Titusville, November (Lutz, Davis, and Leng); Everglade, April (Davis and Grossbeck); Gainesville, September and October, and Monticello, October (Mutchler and Watson). Described from Middle and Southern States.

***Berosus exiguus* (Say)**

Enterprise, Lake Ashby, and Kissimmee, not rare (Hubbard and Schwarz); Biscayne Bay (Schwarz Mss. notes); Lake Okeechobee, May (Davis and Grossbeck); Everglade, May (Davis); Jacksonville, July and August (Roberts Coll.). Described from specimens collected on the shore of Chincoteague Island, Va.

***Berosus striatus* (Say)**

Fort Capron and Tampa, rare (Hubbard and Schwarz); St. Augustine (Schwarz Mss. notes); Florida (Blatchley); Jacksonville, November (Lutz, Davis, and Leng). Described from Pennsylvania.

***Berosus aculeatus* Leconte**

Lake Harney, not rare (Hubbard and Schwarz). Described from North Carolina.

***Berosus peregrinus* (Herbst)**

Included in the Hubbard and Schwarz list, though unseen by them; not since included in Schwarz Mss. notes. Specimens which are doubtfully identified with Herbst's species are known from Fort Myers, March (Davis); Everglade, April (Davis); Monticello, October (Mutchler and Watson); Lakeland and Titusville, November (Lutz, Davis, and Leng). Leconte gave Middle and Southern States as the distribution.

Five species of *Berosus* are described from Cuba and Guadeloupe; none of them are known to be identical with those of Florida.

***Chætarthria pallida* (Leconte)**

Very convex; shining. Head, black. Thorax and elytra, dull brownish yellow; disk of thorax sometimes with a fuscous blotch. Elytra very sparsely and finely punctate; sutural striæ distinct, more pronounced on the apical half. Beneath, black. Length, 1.5-2 mm.

Fort Capron, Sand Point, and Enterprise, not rare (Hubbard and Schwarz); Enterprise, December, in lake shore debris (Brownell). Originally described from specimens collected under stones and in wet places at the junction of the Colorado and Gila rivers, California.

***Helopeltis larvalis* Horn**

Oblong, depressed; piceo-testaceous. Head, obsoletely rugulose. Thorax, at base, nearly three times as wide as long. Elytra with ten punctate striæ; the outer two striæ indistinct; intervals flat. Length, 5.5 mm.

Florida (Roberts Coll. and Leng Coll.); Sarasota, March 4, beneath chunks of debris half buried in the mud of tide water marsh (Blatchley);

see also Beutenmüller, Journ. N. Y. Ent. Soc., VII, p. 176. Described from Louisiana and Sonora. Occurs also in Cuba.

Helochares maculicollis Mulsant

Oblong-oval, distinctly narrowed in front, subdepressed; above brownish yellow. Head with irregular piceous markings. Thorax with large piceous spot on disk. Elytra with ten rows of moderately deeply impressed serrate punctures; intervals flat, finely punctate, the fifth and ninth with a row of coarser punctures. Under surface black or piceous. Length, 4–5.5 mm.

Florida (Horn); Econ. River, March (Brownell). Leconte recorded it from Illinois, Louisiana; Horn gave the distribution as Illinois, Ohio, Kentucky, Missouri, Texas, North Carolina, Florida.

Philhydrus

There are nine species of this genus recorded from Florida. Two of these (*fimbriatus* and *bifidus*) have been placed in different genera by some authors on account of the tarsi on the middle and hind legs being only four jointed; *fimbriatus* is generally smaller, measuring from 4.5–5.5 mm., and the elytra are somewhat coarsely punctate but not striate; *bifidus* measures from 5.5–7 mm. and has the elytra striate, some of the striæ not being entire, while the intervals are flat and punctate. Three of the remaining species are of the various shades usually called testaceous. Of this series, *nebulosus* may be separated by the prosternum being distinctly carinate; the thorax and elytra are indistinctly punctate, the usual rows of coarser punctures being scarcely visible. This species varies in length from 3.5 to 4.5 mm. The other two species in this series do not have the prosternum carinate. They may be partially separated by their sizes: *ochraceous* measures from 3.5–4 mm. and has the mesosternal lamina very feeble, the front edge being arcuate, without distinct angle; *diffusus* measures from 4.5–6 mm. and has the mesosternal lamina prominent with a distinct angular projection. The remaining four species are black or piceous black, sometimes with paler margins. The largest species of this series is *consors* measuring from 7–8 mm.; it is transversely convex with the sides of the elytra nearly vertical; the basal marginal line of the thorax is always distinct; the color of the upper surface is uniformly black. The following three have the margins of the thorax and elytra paler. *P. perplexus* is the smallest, measuring from 4.5–5 mm.; it is subdepressed with sides of the elytra obliquely descending and with the basal marginal line of thorax always distinct. *P.*

cinctus is similar in form to *consors* but smaller, measuring from 6.5–7 mm. and with the basal marginal line of the thorax very indistinct. Finally, *estriatus*, 6.5 mm. in length, was described by Blatchley (Can. Ent. XLIX, 1917, p. 139) who says: "Intermediate in size between *consors* and *perplexus* of Leconte, being smaller and much less convex than *consors* and larger and more broadly ovate than *perplexus*. In both those species the punctation is much coarser, the sutural striæ very distinct and the coarser punctures of elytra in four rows. From *P. cinctus* Say, which it resembles in color, *estriatus* is separated by its less convex form, absence of sutural striæ and oblique front edge of mesosternal crest."

***Philhydrus cinctus* (Say)**

Lake Worth (Slosson in Schwarz Mss. notes); Florida (Blatchley); Lake Okeechobee, April (Davis and Grossbeck). Say, in the original description, says that this species was found in the "Red River of Lake Winnepeck¹; it is also found in Pennsylvania." Leconte gave Middle and Southern States as the range; Horn gave Canada to Georgia and Kansas. The greater part of the Floridian records have been applied to the closely related species, *consors* Leconte.

***Philhydrus consors* Leconte**

Fort Capron, Tampa, and Palatka (Hubbard and Schwarz); St. Augustine, Lake Worth, Crescent City, and Jacksonville (Schwarz Mss. notes); Biscayne Bay, January to March (Slosson Coll.); Lake City, June (Florida Agric. Exp. Sta.). Noted as rare by Mr. Schwarz and not taken by our expeditions. Described from Louisiana. Horn gave the distribution as Louisiana, Florida. This species extends northward, on the Atlantic Coast, to New Jersey.

***Philhydrus nebulosus* (Say)**

Common (Hubbard and Schwarz list); Lake Worth and Biscayne Bay, January to March (Slosson in Schwarz Mss. notes); Florida (Blatchley); Key West, November (Engelhardt); Everglade, April (Davis). Say, in the original description, said he obtained a specimen in the "Lake of the Woods" and it is also listed in the Melsheimer Catalogue. Widely dis-

¹ Lake Winnipeg.

tributed, Canada to California (Horn). Occurs also in Porto Rico, according to Mr. Wintersteiner's determination.

Philhydrus ochraceus Melsheimer

Common (Hubbard and Schwarz list); St. Augustine, Biscayne Bay, Jupiter, and Miami (Schwarz Mss. notes); Florida (Blatchley); Lake Okeechobee, Marco, La Belle, Fort Myers, and Everglade, April, May, and July (Davis); Monticello, October (Mutchler and Watson). Widely distributed, Canada to Mexico (Horn). Described from Pennsylvania. We have Porto Rican specimens that seem to be identical.

Philhydrus diffusus Leconte

Common (Hubbard and Schwarz list); Lake Okeechobee, April (Davis); Punta Gorda, November (Lutz, Davis, and Leng). Described from Nebraska and California. Horn gave only the western distribution, Illinois to California, and described *hamiltoni* from the Atlantic Coast.

Philhydrus perplexus Leconte

Common (Hubbard and Schwarz list); St. Augustine, Haw Creek, and Biscayne Bay (Schwarz Mss. notes); Punta Gorda, November, and Everglade, April, May, and July (Davis). Described from New York, Illinois, Lake Superior, and Nebraska. Widely distributed, Canada to Texas (Horn).

Philhydrus (*Cymbiodita*) **fimbriatus** Melsheimer

Crescent City (Schwarz Mss. notes); Lake Okeechobee, April (Davis). Described from Pennsylvania. Occurs from Canada to Texas (Horn) but may be confused with *rotunda* Say, which occurs from Massachusetts to North Carolina.

Philhydrus (*Helocombus*) **bifidus** Leconte

Enterprise and Orange Co., rare (Hubbard and Schwarz list). Described from Middle and Southern States. Occurs from Canada to Georgia (Horn).

Philhydrus estriatus Blatchley

Type: Dunedin, January and March (Blatchley).

The West Indian fauna includes about a dozen species of *Philhydrus*, occurring in Montserrat, Guadeloupe, Jamaica, Porto Rico, Cuba, and probably other islands. As far as we know at present, only two of these species are identical with the Floridian forms.

Creniphilus

The separation of the species of this genus into groups depends, in part, upon the number of joints in the antennæ which, in view of the small size, is difficult to determine. For this reason we may have included under some species records which may belong to some other species, but notes referring to such identifications will be found in the list of locality records. All of the species are black or piceous and of nearly the same size, measuring 2 mm. or a little less in length and not more than 1 mm. in width. The three species which are said to have the antennæ seven-jointed may be separated in the following manner.

C. reductus (length, 1.6–1.8 mm.) and *degener* (about the same length) have alutaceous sculpturing on the elytra. The former species has the thorax minutely, sparsely punctate, and the elytra relatively coarsely punctured; while the latter has the thorax distinctly, moderately punctate, and elytra without punctures. *C. nanus*, also of same length, has the upper surface polished and finely punctate; form less convex. This (*nanus*) was described as a variety of *ellipsus* (recorded from Arizona) but is said to differ from the typical specimens in being constantly smaller in size and having the elytral punctures relatively coarser. Two others are said to have the antennæ nine-jointed: *suturalis*, 1.5–2 mm. in length, is oblong, fully twice as long as wide, tarsi slender, the posterior pair fully as long as the tibiæ, the pro- and mesosternum without a trace of carina; *depectus*, 1.5 mm. in length, is not much longer than wide, tarsi stouter, the posterior pair shorter than the tibiæ, the prosternum carinate and mesosternum with a small but acute protuberance, elytra distinctly punctate. *C. subcupreus*, 1.5–2 mm. in length, the records for which we have included under *nanus*, is said to have the antennæ eight-jointed.

Creniphilus nanus Fall

Described from Capron and Lake Harney. Specimens from Lake Okeechobee, April and May, and Punta Gorda, Lakeland, and Titusville,

November, have been identified as *nanus* by Mr. F. Wintersteiner. The name *nanus* was proposed subsequent to the publication of the older records; we, therefore, include those for *subcupreus* (Say), which is said by Horn to extend south to Virginia only, under *nanus* as they probably belong to the Floridian insect. They are Biscayne Bay, Crescent City, Enterprise, Lakeland, Everglade, etc., common at various dates.

Creniphilus reductus Fall

Described from Capron; has not been recognized in our material.

Creniphilus degener Horn

Described from Tampa; has been found also at Everglade, April, according to Mr. Wintersteiner's identification.

Creniphilus suturalis (Leconte)

Enterprise, Kissimmee, and Tampa (Hubbard and Schwarz list); St. Augustine and Crescent City (Schwarz Mss. notes); Punta Gorda, Titusville, and Lakeland, November (Lutz, Davis, and Leng). Described from Pennsylvania, New York, and Lake Superior. Horn gave the distribution as Canada to Georgia.

Creniphilus despectus (Leconte)

Haulover, rare (Hubbard and Schwarz). Somewhat doubtfully, we place under this name specimens from Everglade, April, and Salt Marsh (Davis); Lake Okeechobee, April and May (Davis and Grossbeck); Lakeland and Punta Gorda, November (Lutz, Davis, and Leng). As we read Dr. Leconte's treatment of these forms, *despectus* seems to have been intended by him to cover the more southerly forms. The original description gives Middle and Southern States as the distribution. Dr. Horn later associated with this species specimens from Massachusetts, Pennsylvania, Michigan, and Illinois.

The genus *Creniphilus* is known to occur in Cuba and Jamaica, but no descriptions have been published.

Hydrobius tessellatus (Ziegler)

Broadly oval, very convex; pale reddish brown, elytra indistinctly marked with darker brown. Thorax coarsely, not closely, and somewhat irregularly punctate.

Elytra with ten rows of moderately close, but not serrate, punctures; alternate intervals (3, 5, 7, and 9) without trace of the coarse series of punctures. Body, beneath, brownish. Legs brown, basal half of all the femora opaque, punctate, and pubescent. Length, 7–7.5 mm.

Centreville (Roberts Coll. and Schwarz Mss. notes). Described from Pennsylvania. Horn gave the distribution as Canada to Florida. This species is found clinging to the under side of submerged logs.

Hydrobius tumidus Leconte

Oval, very little longer than wide, very convex; piceous black, shining, surface slightly bronzed. Head, closely punctate. Thorax moderately, closely, and equally punctate and with coarser punctures. Elytra with ten rows of punctures; the first and second rows incomplete; alternate intervals (3, 5, 7, and 9) with a row of coarser punctures. Beneath, black. Legs, piceous; tarsi, paler; posterior femora, entirely glabrous, coarsely and sparsely punctate; middle femora, densely punctate and pubescent near the base only; anterior femora opaque, except near the tip. Length, 8–8.5 mm.

Crescent City, Haw Creek, Bartow, and Jacksonville (Schwarz Mss. notes); Lake Okeechobee, in moist humus at edge of lake, April (Grossbeck). Described from New York and Pennsylvania. Horn gave the distribution as New York to Florida.

SPHÆRIDIIDÆ

This family, though not water beetles, is included because they are a part of the Hydrophilidæ in the Henshaw Check List and belong, with that family, to the Palpicornia. They inhabit decaying vegetable matter and are often found on the seashore.

Dactylosternum abdominale (Fabricius)

Oblong-oval, moderately convex; piceous black, shining. Antennæ testaceous, club darker. Head punctate, more finely and densely on the clypeus. Thorax closely punctate, a little more coarsely than the head. Elytra with ten striæ, more deeply impressed on sides and apex; punctures coarse; intervals flat on the disk, slightly convex at apex and sides, closely punctate. Body, beneath, piceous or brownish opaque. Legs, piceo-rufous. Length, 4.5–5 mm.

A native of Brazil, known also from Madeira, Madagascar, Mexico, the Antilles, Florida, and North Carolina (Horn).

Dactylosternum advectum Horn

Oval, slightly oblong; piceous black, shining. Head moderately, closely, and not coarsely punctate, more densely on the clypeus; thorax regularly punctate, a little more closely than the head. Elytra striate-punctate; discal rows fine, and distant outer ones coarser and more deeply impressed; sutural striæ moderately impressed from apex nearly half-way to the base. Body, beneath, piceous or brownish; metasternal area shining, finely punctate. Legs piceo-rufus. Length, 4.5 mm.

Described from Florida. There are two specimens, which have been questionably identified as this species, in the Museum collection from Porto Rico.

Phænotypus palmarum (Schwarz)

The original description of this species is as follows: "Rather broadly oval, convex, piceous black, shining. Antennæ and palpi pale rufo-testaceous. Head minutely, transversely strigose, sparsely punctulate. Thorax minutely alutaceous, sparsely punctate. Elytra sparsely, obsoletely punctate, the punctures confused without tendency to form rows, sutural striæ moderately well impressed from apex one-third toward base. Body beneath opaque. Legs bright rufo-testaceous. Length, .07 inch; 1.75 mm."

The type specimens were collected at Enterprise, on sap of Palmetto, rare (Schwarz). Crescent City (Schwarz Mss. notes); La Belle, Lakeland, Jacksonville, Newberry, and Fort Myers, November (Lutz, Davis, and Leng). Taken by sweeping vegetation, in sifting the ground debris, and at light. Mr. Wintersteiner has recognized this species in material obtained by sweeping in Dominica, W. I. (Lutz).

Phænonotum estriatum (Say)

Rather broadly oval, strongly convex; piceous black, shining. Antennæ testaceous, club fuscous. Head indistinctly punctate. Thorax very finely punctate; punctures of elytra coarser. Body, beneath, piceous, opaque. Metasternal carina shining, sparsely punctate. Legs, piceous. Length, 3-4 mm.

Common (Hubbard and Schwarz); St. Augustine, Lake Worth, Biscayne Bay, and Crescent City (Schwarz Mss. notes); Dunedin, January (Blatchley); Everglade, at light, and La Belle, April (Davis); Lakeland, sifting, and Fort Myers, at light, November (Lutz, Davis, and Leng); Sand Point, February (Roberts Coll.); Monticello, October (Mutchler and Watson); Sanford, May (Van Duzee); Everglade, May and July (Davis). Described from Louisiana. Occurs from Maryland south to Florida and Texas (Horn); also in Guadeloupe, Montserrat, Dominica, Jamaica, and Cuba.

Phænonotum semiglobosum (Zimmermann)

This species is 2.5 mm. in length and is closely related to the preceding, differing only in being smaller and more convex. The entire surface is less distinctly punctate and the elytral punctures are more widely separated.

Common (Hubbard and Schwarz); Crescent City, Haw Creek, Enterprise, Capron, and Tampa (Schwarz Mss. notes); Florida (Blatchley); Lakeland, sifting, Jacksonville, sweeping, and Fort Myers, at light (Lutz, Davis, and Leng). Described from Carolina. Horn gave no records outside of Florida.

Oosternum costatum Sharp

Oval; dull red; scantily covered with a lighter elongate pubescence. Thorax distinctly margined at sides; surface irregularly punctate. Elytra costate; alternate costæ very much raised toward the apex; striæ punctate; intervals pubescent. Metasternum shining, coarsely punctate. Ventral segments with sides dull and impunctate. Length, 1.5–2 mm.

Florida (Slosson Coll.). Described from Mexico, Guatemala and Nicaragua. Occurs also in Porto Rico and Cuba.

Cercyon

C. littoralis occurs in both the Old and New World but has not been found in Florida. It has the outer edge of the front tibiæ emarginate near the apex and with a conspicuous spur near the emargination. The other species recorded from North America do not have this emargination. Of these, five have been recorded from Florida but a number of others are liable to occur, especially among the seacoast species. Although we will not attempt to give detailed descriptions, the following notes may aid the student in separating his species. All of the species recorded from Florida have the sides of the thorax regularly arcuate and narrowed from base to apex. Of these, *nigriceps*, 1.25–2 mm. in length, may be known by having the metasternal area extended by an oblique line which is directed obliquely toward the anterior angle; color piceous, thorax paler at sides, with a distinct basal marginal line; elytra pale, with a piceous transverse band behind the middle. In all of the other species, the metasternal area is limited to the metasternum, the lateral marginal line reaching only to the hind angles. *C. variegatus*, 2–2.25 mm. in length, has the interval between the seventh and eighth striæ of the elytra narrow and with but a single row of punctures; the color is testaceous, except for the head, the median space of thorax and

the humeral space, which are piceous. *C. analis* is of the same size and form as *variegatus* but differs in being piceous black with an indefinite pale space at apex of the elytra. The other two species have the interval between the seventh and eighth striae normally wide and at least biserially punctate. *C. prae-textatum*, 2.5–3 mm. in length, is oval, never very convex, head oblique; elytra piceous black with a large, sharply limited, yellowish white space extending along the sides to the humeral angles; striae rather deeply impressed at apex. *C. floridanum*, 2 mm. in length, is very convex; head vertical; elytra piceous, with a sharply defined apical pale spot which extends narrowly along the sides to base; striae deeply impressed; the intervals convex at sides and apex, scarcely distinctly punctate but the punctures are more noticeable than those of the thorax.

***Cercyon prae-textatum* (Say)**

Common (Hubbard and Schwarz list); St. Augustine, Lake Worth, Biscayne Bay, and St. Lucie (Schwarz Mss. notes); Everglade, at light, April and May (Davis); Fort Myers, March and November, and Monticello, October (Amer. Mus. Nat. Hist. Coll.). Occurs from Canada to Florida and west to Kansas (Horn). There is no locality given in the original description.

***Cercyon anale* Paykull (*ocellatum* Say)**

Capron and Enterprise, not rare (Hubbard and Schwarz). New England to Louisiana (Horn).

***Cercyon floridanum* Horn**

Described from Florida. Capron, Enterprise and Crescent City (Schwarz Mss. notes); Everglade, April and May (Davis); Fort Myers, November, at light (Lutz).

***Cercyon variegatum* Sharp**

Belleair and Jacksonville (Slosson Coll.). Described from North America, Mexico, Guatemala, and Nicaragua. Horn adds New Orleans as a locality record and Mr. Wintersteiner has identified specimens in the Museum collection from Dominica, W. I., as this species.

Cercyon nigriceps Marsham

Punta Gorda (Slosson Coll.). Canada to Louisiana, almost cosmopolitan (Horn). No locality given in the original description. Also occurs in Guadeloupe and Jamaica.

In Hydrophilidæ and Sphæridiidæ we have, thus, 50 species in Florida, of which 13 are also found in the West Indies — possibly more after further study has reduced the doubtful cases. There are 18 genera of which 13 are represented in the West Indies and there are but two West Indian genera (as far as published) not known in Florida. The remarks by the senior author in reference to the Carabidæ of Florida and the West Indies (Bull. Amer. Mus. Nat. Hist., XXXIV, p. 558) might here be repeated in stronger form, for the water beetles of the two regions are surely so very similar that the description of a new species from either region should be preceded by the study of the species of both.

PARNIDÆ.

For the purpose of keeping beetles found in the water together, we include here this small family, the species of which have aquatic habits.

Pelonomus rufescens Casey

Described from Florida and closely related to *P. obscurus* Leconte from the Southern States. In the Roberts Coll. from Bartow, July, and Lake Worth. Under the name *obscurus*, noted as common at Enterprise in the original Hubbard and Schwarz list; from Biscayne Bay in the Joutel Coll., and Daytona, November, in the Engelhardt Coll. Abundant in the debris on the shores of Lake Monroe, November and December (Brownell).

Helichus fastigiatus (Say)

Centreville (Schwarz Mss. notes); Lake City (J. R. Watson). Described from Pennsylvania.

Elmis pusillus (Leconte)

Centreville (Schwarz Mss. notes); Crescent City (Roberts Coll.). Described from specimens found in the Rapids of Niagara.

Elmis foveatus Leconte

Crescent City (H. H. Knight). Described from Santa Fé, New Mexico. The specimens, according to Mr. Knight, are not *foveatus* but indicate a new species near it, the description of which he will publish later.

Stenelmis bicarinatus Leconte

Tampa, one specimen (Hubbard and Schwarz); Crescent City (Roberts Coll.). Found also in Okefinoke Swamp, Georgia, by Prof. J. Chester Bradley. Described from Ohio. The specimens included here indicate a new species near *bicarinatus*, according to Mr. Knight.

Ancyronyx variegatus (Germar)

Crescent City, on sunken logs in cypress swamp (Schwarz Mss. notes). The original description merely gives North America as locality.

Article IV.— A STUDY OF THE ATLANTIC *OCEANITES*

CONTRIBUTIONS FROM THE BREWSTER-SANFORD COLLECTION.— 2¹

BY ROBERT CUSHMAN MURPHY

Plates I to III

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INTRODUCTION

In the spring of 1916, during the course of the Brewster-Sanford Expedition to the littoral of South America, Mr. Rollo H. Beck collected forty-nine specimens of *Oceanites oceanicus* off Bahia, Brazil. Twenty-one of these birds were identified as males and eleven as females. In the cases of twelve more, the sex is doubtfully designated, the symbols on the labels being followed by question marks; in the remaining five instances the collector found the sex quite indeterminable.

The fact that so expert and reliable a field naturalist as Mr. Beck was unable to ascertain, by examination of the gonads, the sex of 35 per cent of these specimens is, in itself, strong evidence of the immaturity of the birds. Careful inspection of the skins has established that every one of the forty-nine is, indeed, a young bird of the year, wearing, therefore, the juvenal plumage—a plumage that has apparently not been heretofore described or even recognized. This discovery has led me to bring together the following data, based partly upon my own field observations and partly upon a study of more than two hundred skins in the collections of The American Museum of Natural History (including the Brewster-Sanford Coll.), the Brooklyn Museum, the Museum of Comparative Zoology, Dr.

¹ See Bulletin Amer. Mus. Nat. Hist., XXXVII, Art. 35, 1917, for the first Contribution.

Jonathan Dwight, and Dr. L. C. Sanford. To the owners and custodians of these several collections, I herewith express my thanks for permission to make use of the material.

To Mr. Howard H. Cleaves I am deeply indebted for permission to publish several of the interesting photographs of petrels which accompany this article, and to Dr. Paul Bartsch, of the U. S. National Museum, and Dr. W. G. Van Name, of the American Museum of Natural History, for examining the stomach contents of *Oceanites* collected in the tropical Atlantic.

PLUMAGES AND MOLTS OF *OCEANITES OCEANICUS OCEANICUS* (KUHL)

Mathews, in 'The Birds of Australia,' allocates the type station of Kuhl's *Procellaria oceanica* to the South Atlantic, off the Mar del Plata. Since I shall demonstrate below, in contravention of Mr. Mathews's expressed opinion, that one and the same form of *Oceanites* occurs in both the North and South Atlantic, migrating from subantarctic breeding grounds to the coast of Labrador or beyond, I employ here the trinomial of the Atlantic race, the name which is applicable to the bird of the American Ornithologists' Union 'Check-List.'

The grayish-black nestling of *Oceanites oceanicus* has been described by Hall (1900) and others. In agreement with most small Tubinares, this species passes from the downy stage into a plumage substantially resembling that of the adult but differing, as I shall now show, in several particulars. In the first place, juvenal birds, as exemplified by the Bahia specimens, and others, have fresh, black, unworn quills and body feathers, and gray, white-edged greater coverts, at a time of the year when the feathers of old birds show the maximum effects of wear and fading. But the juvenal birds differ just as definitely from adults in new plumage — that is, from adults taken in the northern autumn after completion of the annual molt — for, in a greater or less degree, each of the forty-nine Bahia skins and each of a small series of juvenals from other, widely separated localities is characterized by *conspicuous white edgings on the feathers of the belly, and by a whitish spot in the lores*. When we add to these striking features the fact that young birds, at least up to the middle of their first summer (July), have relatively weaker bills than the adults, with a less pronounced unguis, slighter bones in the tarsi and wings, and smaller claws on the toes, we have a combination of characters by which birds of the year may be recognized until they have attained full growth, which seems to be within six or seven months of hatching. Thereafter they can still be distinguished by conditions of the plumage to be described below.

The Bahia birds were collected on April 15, 27, 28, and May 1, 1916, which implies that they can have been hardly more than two months out of the nest. Practically all of these specimens have slightly shorter wings and tails, and smaller bills, than mature birds collected by the writer at the same season and in nearly the same latitude, but further offshore. They show like indications of immaturity when compared with adults from many other points in the South and North Atlantic; but, on the other hand, they agree in appearance and dimensions with other juvenal specimens collected at approximately the same season of the year in both near and distant localities. As might be expected, they resemble in all particulars eight young birds in the collection of the Museum of Comparative Zoology which were taken at Rio Janeiro in May 1865 by J. A. Allen and N. Dexter.

In general, the feathers of sea birds undergo relatively slight disintegration when compared with those of terrestrial species; but a study of all the juvenal specimens of *Oceanites oceanicus oceanicus* at my disposal shows that the new, soft plumage is subject to rather rapid fading and wearing away, especially after the end of April. Whereas adults collected even several months after the molt are often without noticeable traces of wear, except near the bend of the wing where the feathers undergo constant abrasion during the flexure, the juvenals show much more pronouncedly the destructive effects of aging. The sequence of the changes may best be expressed by a description of specimens illustrating successive stages.

First stage. The forty-nine Bahia skins are very uniform as regards freshness of plumage, the feathers being perceptibly blacker and less frayed than those of juvenals taken only six weeks later in the year. The series exhibits considerable differences in size, as will be shown below; some specimens may well be a number of weeks older than others, for the breeding and nesting season of *Oceanites* is known to stretch through a period approaching five months. In all of these skins, the whitish tips of the greater coverts form a distinct band on the wing. The white edgings on the feathers of the belly are always present, though their extent varies from a small patch to an area covering the entire ventral surface caudad from the breast. The loreal spot is formed by prevailing white feathers in this region. In most of the birds this spot is conspicuous, but in a few it is obsolete. Apparently, it ultimately becomes concealed by an overgrowth of the feathers in front of it.

Second stage. A single juvenal, taken off the coast of the French Congo on June 20 (cf. p. 126), resembles the April and May Bahia skins but is somewhat bleached and worn. The white margins on the belly are inconspicuous because the feathers have frayed out. The white spot in the lores, however, is prominent. The quill feathers have begun to disintegrate at their edges.

Slightly more advanced in growth, but showing rather less general wear of the plumage, is a specimen from the coast of Massachusetts (L. C. Sanford Coll., 4089, ♂, 7 miles E. N. E. of Pigeon Cove, July 1, 1911). This bird has a well-marked, though small, area of white edgings on the belly, but the loreal spot is partly concealed. The rusty tinge on the under surface shows the result of two full months of longer life than the Bahia birds.

Third stage. Two specimens from Long Island, N. Y. (Amer. Mus. Nat. Hist., 68167, ♀ Aug. 2, 1891, and Brooklyn Mus., 11050, ♀?, Aug. 8, 1915) show decided effects of wear and weathering. The entire plumage is of a dingy, threadbare aspect and the whitish edgings have abraded away from the greater coverts, leaving the latter bleached and frayed. Considerable disintegration has taken place in the vanes of the remiges. The white edgings of the ventral feathers and the white mottling of the lores are still discernible.

From this point onward, I am unable to trace with certainty the plumage changes of juvenal *Oceanites*. North Atlantic specimens of first year birds are rather rare in the collections that I have examined, and it will be necessary to await an opportunity to study September, October, and November juvenals before the season of the first molt can be positively determined. August specimens show no trace of the beginning of a molt, whereas most adults practically complete the process before the end of that month. I am strongly of the opinion that the birds do not molt at all during their first year but retain their juvenal feathers until the second spring. On this hypothesis I interpret the following facts. (1) The old quill feathers of most adult migrant *Oceanites*, collected before or during the summer molt, are relatively only slightly abraded, in spite of the many months of wear that they have undergone. (2) Certain summer birds, however, which have already acquired by molt most of their adult plumage, have the old primaries and rectrices extraordinarily worn and faded, presenting, therefore, a strong contrast to the usual condition and an apparent exception to the general rule that the flight feathers of pelagic birds show only slight or negligible effects of wear. Now the status of such birds as come under this second heading may be explained on the assumption that they are yearlings undergoing their first molt. The last few months of more than a year's wear would be expected to prove highly destructive to a juvenal quill. The result of attrition in the primary feathers of certain specimens so greatly exceeds the effect visible in other specimens that one may circumstantially correlate the difference with a difference in age of the respective groups of birds.

The sequences of plumages of the adult *Oceanites* are shown very clearly in a series of skins now before me. To begin with breeding specimens,

twelve birds from the island of South Georgia (December to February) have only moderately worn plumage, except that the greater coverts of the wing are much frayed and show almost no trace of white or gray edgings. The feathers of the under surface are rather rusty.

April adults from the tropical South Atlantic resemble the South Georgia birds, but, as might be expected, the wear and fading of the contour feathers have progressed a step further. I can find no sign of incipient molt in any one of eight skins. A specimen from the western North Atlantic (Amer. Mus. Nat. Hist., 55092), taken on May 5, has still shabbier body plumage,

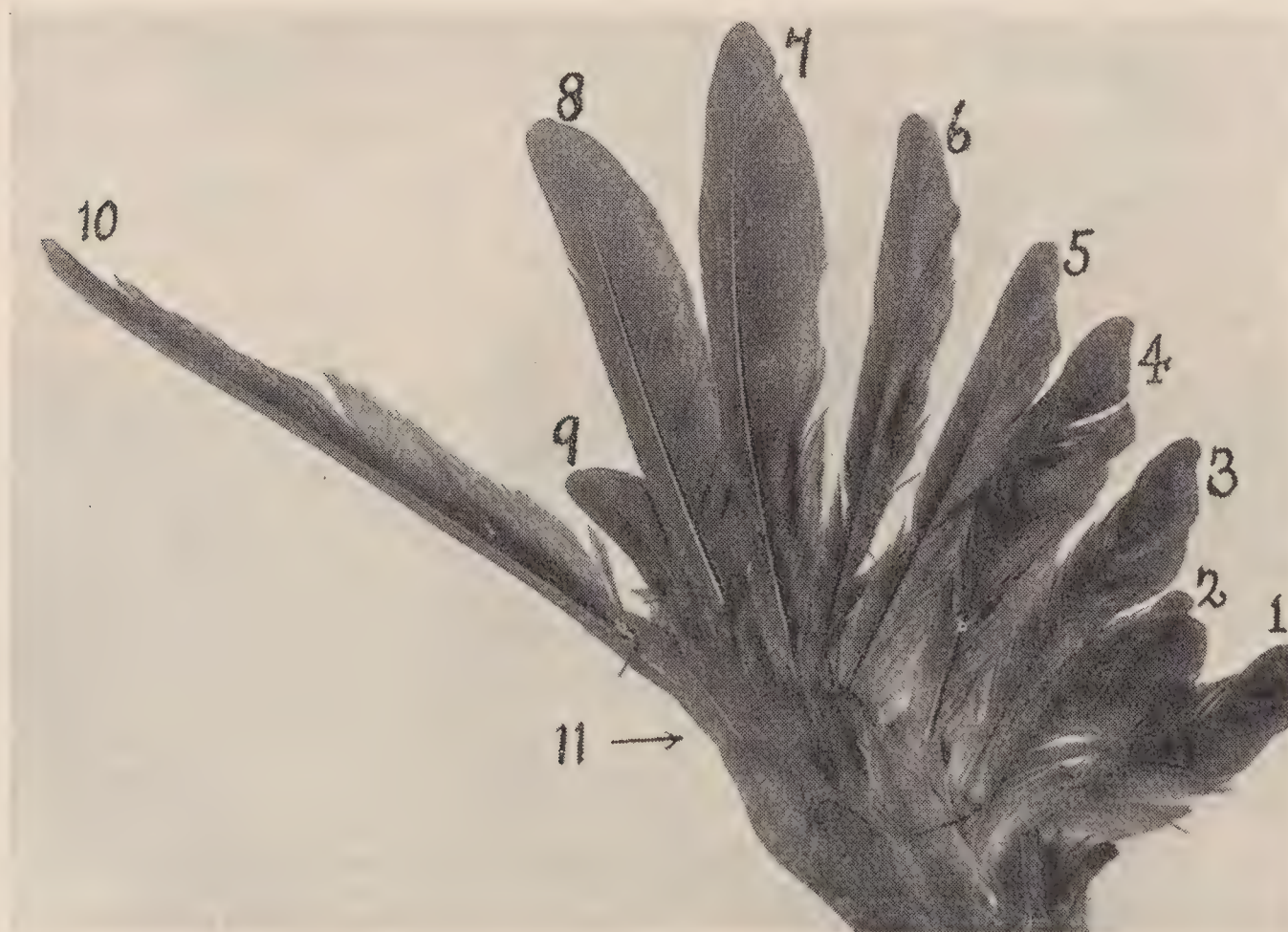


Fig. 1. Molting wing of *Oceanites* (Brooklyn Mus. 11048, Long Island, N. Y., Aug. 8, 1915). The tenth (outermost functional) primary is an old quill, the others are new; only the first (innermost) has attained its full growth. If the tenth primary also had been dropped, the wing would have appeared abnormally short, and the seventh quill would have been for some time the longest.

although the quills are in surprisingly good condition. This bird, too, had apparently not commenced its molt when it was taken.

In two examples collected off Cape Hatteras on June 15, we finally see the molt well under way. One of these (Amer. Mus. Nat. Hist., 96855) has the first, new, ensheathed feathers scattered through the old plumage of its breast and back. It has lost several of its old secondaries, as well as the innermost primaries, and these are being succeeded by young quills. At the same time, new, grayish, greater coverts, with broad white edges, are appearing.

A series of birds taken between July and September along the coasts

of New York and New England shows that the loss and replacement of the flight feathers is finished by about the end of August but that the renewal of the body plumage is slow and irregular and may not be wholly accomplished before the end of September. The remiges are lost before the rectrices, the primaries dropping out approximately by twos (i. e. one in each wing) from the inner towards the outermost feathers, which are the last to go. The order of molt of the tail feathers is, in general, from the central towards the outer feathers nearly or quite symmetrically, the coverts molting at the same time.

Completion of the primary molt leaves *Oceanites* excessively short-winged. Several August specimens before me have wing-lengths of only 130 mm., which is fully 25 mm. shorter than the maximum, and about 15 mm. shorter than the average, for wings with full-grown primaries. Growth after the molt requires at least a month, for not until the last of September is the normal proportion of the primaries (outermost = third from outermost) restored and the wing length again equal to its measurement before the molt. The bird then has its best physical equipment for the long migration to the breeding grounds.

Salient features of the molt are well illustrated by several of the photographic illustrations published with this article. Before closing the discussion, it remains only to speak of the irregular white markings which frequently appear in the Atlantic *Oceanites*. Some of these are perhaps albinistic, as where specimens from many localities have one or more prominent white feathers on the back, breast, or head. Another case, more difficult to explain, is exemplified by September birds from the eastern tropical Atlantic (Amer. Mus. Nat. Hist., 132474 and 132477) which have white spots on the ends of the outermost rectrices on each side.

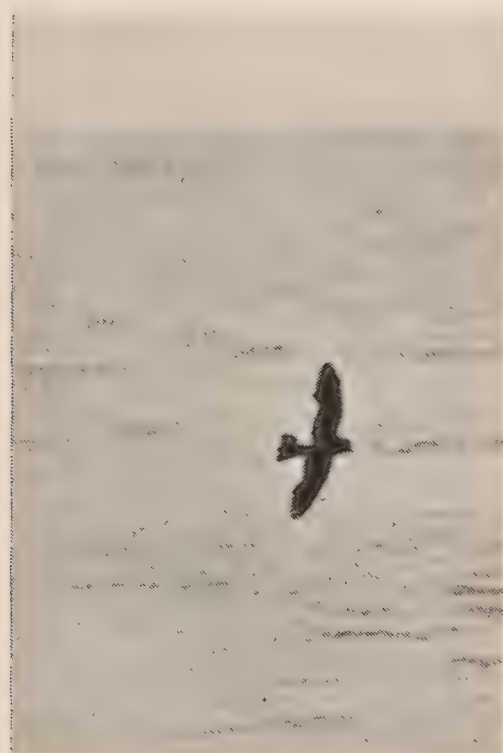
TAXONOMIC STATUS OF THE ATLANTIC BIRD

Mathews (1912) states his conclusions concerning the Atlantic *Oceanites* in the following words:

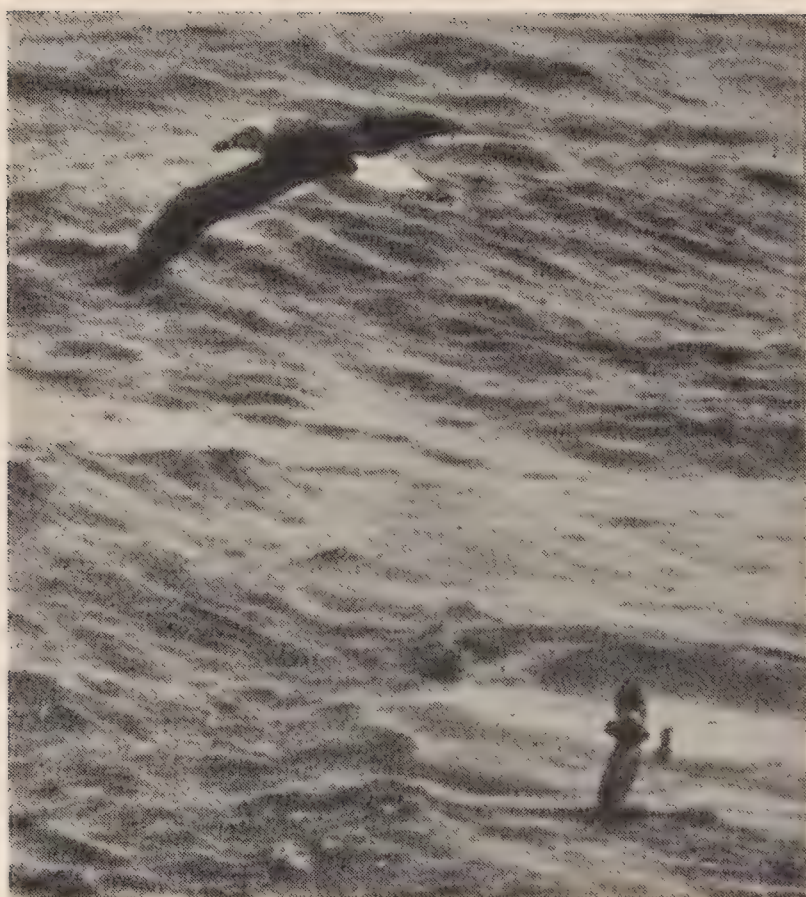
Bonaparte named the North Atlantic form *Procellaria wilsoni*, and recent students have accepted this as a synonym of *O. oceanicus*, typical, concluding that the bird breeding in the Antarctic circle ranges north and becomes common in the North Atlantic in the Antarctic winter, i. e., the northern summer. From my researches I conclude that this is an unsatisfactory explanation, and confidently anticipate the discovery of breeding colonies of a subspecies of *O. oceanicus* on some of the West Indian or North African islands, which would bear the name of *O. o. wilsoni* (Bonaparte).



2



3



5



4

Figs. 2 and 3. *Oceanites* in the wake of a steamer. Photographed between New York and the West Indies, May 27 or 28, 1912. The molt of the distal secondaries and proximal primaries shows clearly in the bird in Fig. 2.

Fig. 4. *Oceanites* in the wake of the brig *Daisy*, lat. $21^{\circ} 56' S.$, long. $35^{\circ} W.$, Oct. 27, 1912. Completion of the growth of the remiges is indicated by the even edge of the wing, as contrasted with the nicked wing of the bird in Fig. 2. The new, white-tipped greater coverts form a distinct band.

Fig. 5. *Oceanites* in lat. $44^{\circ} 57' S.$, long. $39^{\circ} 51' W.$, Nov. 16, 1912. The bird in the background is an albatross (*Thalassogeron culminatus*).

From the foregoing discussion of the molt and growth of feathers, it is evident that very great variation in length of wing and tail is to be expected among the Atlantic examples of *Oceanites* captured during the half-year which contains the summer of the northern hemisphere. Being forearmed against possible confusion from this source, consideration of a summary of the measurements of ninety-seven specimens taken in the Atlantic between 55° south latitude and 50° north latitude, and between 8° east longitude and 75° west longitude, will be of interest.

The first specimens listed in Table I are the 12 adult birds collected at South Georgia during the breeding season of the antarctic summer. Eleven of these were taken by the writer between Dec. 1, 1912 and Feb. 6, 1913; the other is dated Feb. 10, 1914. All were probably breeding birds, for the sexual organs were enlarged, and two of the males (Amer. Mus. Nat. Hist., 132480, and Brooklyn Mus., 10718) are specifically stated to have had bare brood-patches on the belly. Variation in the length of wing, tail, and culmen, which are the three structures ordinarily showing the greatest range in dimensions, is relatively less than that found among pelagic migrants, such as make up the bulk of the average museum series of *Oceanites*; but this fact is merely an expression of the uniformity, as regards state of plumage and maturity, that breeding birds might be expected to exhibit.

The second series in the table comprises twelve birds collected by the writer at two stations in the tropical Atlantic and at diametrically opposed periods of the year. Four of these were taken in the vicinity of 12° 30' north latitude and 25° west longitude, south of the Cape Verde Islands, on Sept. 23 and 24, 1912. The remaining eight are from 3° 15' south latitude and 33° 40' west longitude, northeast of Cape San Roque, Brazil, and were shot on April 19, 1913. The average measurements of both males and females of this small series are very close to those of the South Georgia specimens, the only noticeable, though slight, discrepancies being the greater average length of wing and tail in the tropical females — a condition wholly produced in this instance by pronounced individual variation in two out of the eight April birds. As suggested above, a wider range between the maxima and minima of wing and tail dimensions is generally to be expected of birds collected at sea than of breeding examples.

The third set of measurements refers to the juvenal, Bahia specimens in the Brewster-Sanford Collection and, in interpreting these, we must consider the factor of uncompleted growth as of more importance than those of individual or seasonal variation. A casual examination of these birds, some of which are characterized by short wings, puny bills, and strikingly delicate tarsi, indicates that many had not yet grown to their full size,

TABLE I.—SUMMARY OF MEASUREMENTS OF 97 SPECIMENS OF OCEANITES FROM THE ATLANTIC

		WING	TAIL	EXPOSED CULMEN	WIDTH OF BILL AT BASE	TARSUS	MIDDLE TOE AND CLAW
		<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
7 males from South Georgia	Minimum	142	60	11.9	6	34	26.4
	Maximum	148	66.4	13	6.6	36	28.7
	Average	145.7	62.2	12.5	6.3	34.8	27.7
5 females from South Georgia	Minimum	140	59.6	11.8	6	33.1	26
	Maximum	146	68	13	6.5	36	28
	Average	144	62.9	12.5	6.2	34.4	27
4 males from the tropical Atlantic	Minimum	141	60.5	12.3	6.2	33.6	26.5
	Maximum	152.6	64	12.8	6.6	35.2	28
	Average	144.9	62.3	12.7	6.5	34.5	27.3
8 females from the tropical Atlantic	Minimum	144	62	12.3	6	34	26
	Maximum	154.5	69	13.1	6.8	36	29.6
	Average	147.7	64.9	12.8	6.5	34.8	28.1
21 males from Bahia, Brazil	Minimum	136	56.5	11.5	4.9	32	25.3
	Maximum	149	68	13	6.7	36.7	29.6
	Average	143.1	61	12.2	5.8	34.7	27.1
11 females from Bahia, Brazil	Minimum	136.5	57.5	11.5	5.2	31.3	26
	Maximum	151	66	12.8	6.4	36.1	28
	Average	143.8	62.4	12	5.8	34.1	26.8
1 female from the French Congo		140	62.2	11.1	6.2	32.7	25.8
2 males from the southern coast of the United States	Minimum	142	64.5	12.7	6.7	35	27.2
	Maximum	143.7	66.2	13	6.8	35.4	28.2
	Average	142.9	65.4	12.9	6.7+	35.2	27.7
2 females from the south- ern coast of the United States	Minimum	146	67.2	12.8	6.1	34	27.2
	Maximum	149.4	69	13.2	6.7	34.6	28
	Average	147.7	68.1	13	6.4	34.3	27.6
12 males from Long Is- land, N. Y.	Minimum	137.4	58.3	11.6	5.7	33	25.8
	Maximum	150	66.5	13	6.5	36.4	29.6
	Average	144	62.7	12.4	6.1	34.4	27.2
9 females from Long Is- land, N. Y.	Minimum	140	57	12	5.9	33.7	26.7
	Maximum	155.5	68	13.2	6.7	36.8	30
	Average	146.2	62.8	12.5	6.2	35	28
9 males from the coasts of New England and New- foundland	Minimum	137.5	59	12.6	5.9	33.6	27
	Maximum	148	65	13	6.9	35.7	29.2
	Average	143	62.7	12.7	6.4	33.7	28.1
6 females from the coasts of Massachusetts and Maine	Minimum	141.6	63	12.4	5.5	33.6	26.3
	Maximum	153	73	13.2	6.9	35.5	29
	Average	145.5	66.4	12.8	6.3	34.7	27.7

an inference confirmed by the low minimum figures in the columns of the thirty-two specimens tabulated. Nevertheless, the maximum dimensions of the most advanced birds in the series fully equal those of adults in fresh plumage and so serve to pull up the averages. The interesting point is that, if only the *average* measurements of these thirty-two juvenals were considered, the unusually low figure for the mean width of the maxilla at its base would alone give a clue to the immaturity of the specimens. In *Oceanites* the total extent of variation in the width of the bill may equal 32 per cent, or approximately one-third, of the average width. I have found that slow development of the bill is typical of many other Tubinares as well, and it is easy to mistake for taxonomic distinctions variations in the structure of this organ which are in reality due to age.

The fourth set of measurements is from a single female petrel (Amer. Mus. Nat. Hist., Belgian Congo Exp. Field Cat. No. 1) collected by Messrs. Lang and Chapin off the coast of French Equatorial Africa, on June 20, 1909. This specimen is small and it has an extremely weak unguis on its bill. These features, added to those of its juvenal plumage (cf. p. 119), give the skin a sufficiently different facies from the well-known adult form of *Oceanites oceanicus oceanicus* to serve an ornithologist who was unacquainted with the characters of the juvenal bird as the type of a new race. Fortunately, the skins from Bahia furnish the key to a comprehension of the African specimen's status: the latter proves to be wholly comparable with other young birds collected while on their first northward migration.

In the fifth series of measurements, we deal with four specimens from the southern Atlantic coast of the United States (Amer. Mus. Nat. Hist., 55091, 55092, 96854, and 96855). One bird of each sex was taken on May 5, 1887, in latitude 26° N., on the route to Pará; the other pair was collected off Cape Hatteras, N. C., on June 15, 1913. Both males chance to have rather short wings, but nothing in the appearance or dimensions of any of the four specimens suggests that they are to be differentiated from tropical or subantarctic representatives. The same statement applies with equal force to the petrels included under the sixth and seventh groups of the table. Here are summarized the measurements of thirty-six birds collected on the coast of New York, New England, and the Maritime Provinces, between the dates of July 1 and September 10. It is during this period that the major part of the molt of remiges and rectrices is undergone, but I have excluded figures referring to birds which had within a brief time dropped the last primary. The maxima and minima therefore represent chiefly the range of individual variation and the effect of wear.

Further evidence in favor of the racial unity of Atlantic birds from widely scattered localities is to be found in the close approximation between

the average measurements of the seven groups of skins which I have used in the statistical treatment and the figures denoting the mid-point between the extreme measurements in the same series of specimens. This is shown in the following table, together with the percentum ratio of the total extent of variation to the averages for each structure. In preparing this table, the sexes have not been segregated, because the data before me give no hint of a constant sexual discrepancy in size.

TABLE II

	WING	TAIL	EXPOSED CULMEN	WIDTH OF BILL AT BASE	TARSUS	MIDDLE TOE AND CLAW
	mm.	mm.	mm.	mm.	mm.	mm.
Average of the 12 sets of averages in the table on p. 125, based upon 97 specimens of both sexes, including juvenals.	144.9	63.7	12.6	6.3	34.6	27.5
Mid-point of range of measurements of 97 specimens.	145.8	64.8	12.2	5.9	34.1	27.7
Variation on either side of mid-point.	9.8	8.3	1.1	1.	2.8	1.4
Minima of 97 specimens.	136 ¹	56.5	11.1	4.9	31.3	25.3
Maxima of 97 specimens	155.5	73.8	13.2	6.9	36.8	30
Percentage of the average to which the total extent of variation amounts.	14%	26%	17%	32%	16%	10%

From all of the above, it appears that we have exact quantitative evidence for believing that a form of *Oceanites* referable to a single subspecies ranges through both the North and South Atlantic Oceans. The specimens studied comprise birds killed during every month of the year excepting March, October, and November, and the observed variation in color and condition of plumage, as well as the range in size and the places of capture, are most

¹ Immediately after molting the outermost primary, some birds have wing-lengths as low as 130 mm.

reasonably explained not by Mr. Mathews' theory but on the generally accepted hypothesis of a post-nuptial migration of the Atlantic birds to the northern ocean from breeding grounds in the Far South.

South Georgia may be positively designated as a nesting station of typical *Oceanites oceanicus oceanicus* (Kuhl), although we have no present means of knowing where the bulk of the incalculable myriads of *Oceanites* in the Atlantic has its source. Since *Oceanites* breeds also at the South Orkneys, and presumably at Bouvet Island in the eastern South Atlantic, the South Sandwich group, and in parts of the American quadrant of the antarctic mainland, it is quite within the range of likelihood that some future "student of speciation," to use a phrase now popular among California naturalists, may be able to demonstrate a constant differentiation, which would have evolutionary significance, between the South Georgia representative and birds breeding elsewhere. Clarke (1913) describes the terrifically severe struggle for existence to which the breeding Wilson's petrel of the South Orkneys is subjected, and it might be supposed that such a factor would tend to accelerate and fix variations of taxonomic worth. In the meanwhile, however, any attempt to draw subspecific distinctions upon the basis of Atlantic specimens obtained through pelagic collecting would be worse than useless. In dealing with such variable avian species as *Oceanites oceanicus*, large series of birds collected at the various breeding grounds, preferably on the nests, would be the only safe materials for a revision of the systematic relationships.

Breeding specimens of *Oceanites* being scarce in collections, it is desirable to publish here the full data for the 12 South Georgia skins. The number is, of course, too small to cover the probable extent of variation (Lönnerberg (1906), in fact, records the wing-length of one breeding male from South Georgia as 138 mm., which is lower than in any of my specimens), yet it is unlikely that the addition of even a very much larger number of skins would substantially change the *average* measurements of the twelve examples listed in Table III.

Even aside from the conclusions that I have drawn from a taxonomic study, Mathews' confident belief that breeding colonies of a subspecies of *Oceanites oceanicus* remain to be discovered on some of the West Indian or North African islands surely has less to substantiate it now than it had when he committed his faith to print. The Antilles have been raked over with considerable thoroughness and several expert ornithologists have recently made independent explorations there in special search of Tubinares. Bannerman (1914) has published his admirable studies on the petrels of the North Atlantic islands and has shown that *Oceanites* is no more than a straggler or visitor at the various insular groups between the Cape Verdes

TABLE III. — MEASUREMENTS OF BREEDING SPECIMENS OF OCEANITES OCEANICUS

COLLECTION AND NUMBER	SEX	LOCALITY	DATE	COLLECTOR	WING	TAIL	EXPOSED CULMEN	WIDTH OF BILL AT BASE	TARSUS	MIDDLE TOE AND CLAW
A. M. N. H., 132479 Brooklyn Mus., 10714	♂	South Georgia	Dec. 1, 1912	R. C. Murphy	mm. 146.5	mm. 66.4	mm. 13	mm. 6.4	mm. 34.5	mm. 28
A. M. N. H., 132480	♂	"	"	"	142.5	60	12	6.6	35.8	26.4
A. M. N. H., 132482	♂	"	Jan. 30, 1913	"	142	61	12.5	6.3	34	28.7
A. M. N. H., 132481	♂	"	Feb. 6, 1913	"	147	60	13	6	36	28.7
Brooklyn Mus., 10718	♂	"	"	"	148	62	12	6.4	34	26.7
Brooklyn Mus., 10717	♂	"	"	"	146	63	11.9	6	34.6	28
A. M. N. H., 132483	♀	"	Dec. 1, 1912	"	148	63.2	12.8	6.1	35	27.6
Brooklyn Mus., 10715	♀	"	"	"	145	64	12	6.5	35.2	28
Brooklyn Mus., 10716	♀	"	Feb. 6, 1913	"	144	59.6	12.9	6.1	36	26.7
A. M. N. H., 132484	♀	"	"	"	145	62	11.8	6.1	33.7	26
Brooklyn Mus., 11179	♀	"	Feb. 10, 1914	J. G. Correia	140	61	12.7	6	34	28
					146	68	13	6.3	33.1	26.4

and the Azores.¹ If further testimony be needed to prove beyond a doubt that the Atlantic *Oceanites* has its nesting grounds exclusively in the Far South and that it does make migrations of tremendous extent — regardless of how restricted in distribution certain other races of Tubinares are known or believed to be — the following personal log of the observed migration of the bird will supply it.

MIGRATION OF THE ATLANTIC OCEANITES

In 1912 and 1913, the writer made a voyage to South Georgia under the auspices of the Brooklyn Museum and The American Museum of Natural History. Migrating Wilson's petrels were observed throughout most of the itinerary, which was as follows.

I left New York on a Quebec Line steamer on May 25, 1912, arriving at St. Thomas, W. I., on May 31 and at Barbados on June 8. On the 17th of the latter month I joined the New Bedford whaling brig *Daisy*, which proceeded to Dominica. Beginning on July 2, we cruised for four weeks in the waters about Dominica and Martinique, and then started northward, passing Sombrero on Aug. 2. On Aug. 18 we reached latitude 32° N., in approximately 58° west longitude, and then turned sharply towards the east. Between Sept. 16 and 18 we lay in the harbor of St. Vincent, Cape Verde Islands, and on Oct. 16 made a call at the Brazilian island of Fernando Noronha. Thereafter we sighted no land until Nov. 23, when we reached South Georgia in latitude 54° S. On March 15, 1913, we began the northward voyage and saw land only once, Trinidad Islet in 20° 30' south latitude, until we arrived again at Barbados on May 8. From here I took the first steamer home, reaching New York on May 24, 1913.

The approximate track of the *Daisy's* cruise is shown on the map on p. 131, and the daily reckonings of the brig's position for the greater part of the voyage are recorded in Table IV.

On the morning of May 26, 1912, just after we had left New York, Wilson's petrels picked up the track of the steamer, and they followed us throughout the first fifteen hundred mile lap of the journey, which brought us within sight of Culebra, W. I. This was on May 30, and between that date and Sept. 23, in latitude 12° 46' N., longitude 25° 05' W., I met with

¹ In a popular book, 'Birds That Hunt and Are Hunted,' 1899, the author, Neltje Blanchan, states (p. 71) of *Oceanites oceanicus*, "In the latter month [February] the author has seen the birds in great numbers off the Azores, but, unhappily, not on them. . . .; however, it is not unlikely they nest on these islands. . . ." There is no assurance that the author was capable of distinguishing *Oceanites* in flight from *Thalassidroma pelagica* or one of the species of *Oceanodroma*. Indeed, few persons have had sufficient field experience with the birds to make this discrimination at ordinary distances.



Fig. 6. Base map of the Atlantic showing the approximate course of the brig *Daisy* during the South Georgia Expedition of 1912-1913 and the collecting stations (designated by black dots) of the specimens of *Oceanites* used in the preparation of this paper.

no examples of *Oceanites*. During the interim I had travelled from the southern Antilles northward over the course stated above, and eastward across the Atlantic.

Quiet weather, even long, monotonous calms, characterized the sub-tropical summer of our North Atlantic cruise, so that conditions were favorable for pelagic observations; but, although I spent many hours at the masthead of the whaleship and noted other birds, including two species of Tubinares, I saw no Wilson's petrels until we met them late in September, as southward-bound autumn migrants, south of the Cape Verdes. Here, on Sept. 23, in the latitude given above, I shot three specimens and saw others.

From this date forward, throughout the course of the South Georgia Expedition, Wilson's petrel was noted almost daily. The remarkable record of observed migration, with exact oceanic positions, is summarized in Table IV. For a period of sixty-three days on the southward journey, *Oceanites* was recorded on all but two. During fifty-five days on the northward trip, the species was not observed on a total of fifteen days, but these were well scattered through the entire period. Between Barbados and New York, in May 1913, the birds were again seen almost daily. The extent of this single established record of continuous migration covers, therefore, 90 degrees of latitude, and the breadth of the tropical Atlantic. It should prove beyond all doubt that the *Oceanites* of the North and South Atlantic is one and the same.

The following pelagic notes are drawn largely from my field journal. The latitude and longitude of the numerous records have been omitted, but may be determined by comparing the dates with those in Table IV.

On May 26, 1912, the day after the steamer had left New York, about a hundred Wilson's petrels pursued us until dark. During the second day they dwindled off to a dozen, but next morning they were with us in countless numbers. As far as the eye could reach they stretched astern, coursing back and forth, dipping and rising with the undulations of the sea, crossing and recrossing our wake, but never wandering more than a few hundred feet on either side. When they turned, their wing tips sometimes cut the water; only rarely would a bird rise as high as the horizon and stand out for an instant against the sky. Fully half the time they glided on rigid wings, and even when they beat the wings it was in a gentle and leisurely manner; yet we were making fourteen knots an hour. The petrels, with their zig-zagging and circling, flew at least three times as far.

The main front of this black-and-white army kept itself about twenty yards astern but two or three individuals repeatedly flew alongside so closely that they almost brushed the rail, going ahead as far as the broken

water at the bow and then dropping behind. The high-browed heads were drawn in close to the breast, the bills pointing slightly downward. The feet, with webs closed, extended straight out beyond the tail. Whenever a bit of food was cast over from the steamer, or whirled from beneath the screws, the petrels, with spread tails, and feet "pumping" together, descended one in the track of another and hopped and danced merrily on the very top of the insubstantial ocean. As the vessel drew away from such a hungry group — a flurry of long, raised, fanning wings and white-banded bodies — they looked not like birds, but rather like flocking butterflies. They probably overlooked nothing edible in their course, so thoroughly did they scour about, and whenever one dropped to enjoy its find the others congregated at the signal. Frequently they fell back out of sight while feeding.

By sunset each day the ranks of the petrels were greatly thinned out and by half past seven o'clock, at the latest, even the most persevering had dropped behind. On the calm evening of the third day at sea I actually saw the last few birds drop onto the ocean. In the morning they rarely overtook us before eight o'clock. How did they find us again? Certainly not as Mosely (1892) says, by "tracing the ship up again in the early morning by the trail of *débris* left in its wake." If the petrels rested from eight o'clock in the evening until three next morning, we would have gained a hundred miles. And, considering the rapid dissipation of the refuse from a steamer, particularly when the Gulf Stream is crossed, there would be no trail that even a bird could follow. It is possible that the petrels located us by merely continuing a straight course. There is the perhaps more likely alternative that we were followed not by the same band for the whole trip, but by new ones made up each morning of roving birds. I have presented evidence (1914), however, to show that in the South Atlantic our whaling brig was sometimes pursued by the same individual *Tubinares* for days together.

After noting the petrels near Culebra, there comes a break in my journal of the species until autumn, in the eastern Atlantic. Much of what follows is taken verbatim from my notebook, without even a change of tense.

Sept. 23, 1912. Excessively hot and calm. At 8 A.M. several Wilson's petrels were seen, so I lowered the dory and shot three, along with a specimen of *Stercorarius parasiticus*. The petrels were about all day, feeding wherever there was a "slick" upon the surface. They did not come near the brig. Their "walking on the water," as I observed it, is not strictly a walking or running — one foot after the other — but rather a two-footed hopping or pattering, both webs coming down together as they spring along the surface.

The last sentence expresses my entire experience as regards the "walking" of *Oceanites*. Portrayers of birds, from Audubon to Fuertes, have drawn this petrel with the legs in an alternating, or truly running position, and the much used term "walking on the water" surely gives a mental picture of foot-after-foot progression. In 1907 I first noticed that Wilson's petrels feeding in New York Harbor did not "walk" in the expected manner, although they often "stood" on the water. Since then I have been partic-



Fig. 7. *Oceanites* feeding in the Lower Bay of New York, a quarter mile northwest of the extreme point of Sandy Hook, N. J., in early August, 1915. Photographs by Howard H. Cleaves.

ularly keen to observe this point, but I have never yet seen one "walk" or "run." It is of interest that Mr. Cleaves' photographs of Wilson's petrels, including a reel of cinematograph scenes, show the birds in every attitude of "hop, skip, and jump," but never progressing foot after foot.

Negative evidence is, of course, seldom conclusive, but if it be true that *Oceanites* never "walks," possibly *Thalassidroma* does. The original "walking" story is that of Dampier (1703), and it doubtless refers to birds

of one of the two genera named above, or to *Oceanodroma*. He wrote (Voy. III, pt. 1, p. 97): "As they fly . . . they pat the Water alternately with their Feet, as if they walkt upon it; tho' still upon the Wing. And from hence the Seamen give them the name of Petrels,¹ in allusion to St. Peter's walking upon the Lake of Gennesareth."

Sept. 24. Calm. Six Wilson's petrels seen. They did not come near the almost motionless brig, but flew about singly.

Sept. 27. Wilson's petrels seen in company with *Oceanodroma leucorhoa* and a race of *Æstrelata mollis*. Elsewhere (Auk, 1915, pp. 171-172) I have described the striking difference in the usual style of flight of *Oceanites* and *Oceanodroma*. The latter "flies with rapid, 'leaping' strokes, quite unlike the alternations of gliding and synchronous flutters which characterize the flight of *Oceanites*. An observer who has once had the good fortune of watching the two species together can thereafter distinguish them almost as far away as the birds can be seen" (Murphy, loc. cit.).

The Wilson's petrels are difficult to see against water ruffled by the wind, and they seldom rise above the horizon of a person standing on the deck of a ship. They therefore often rush into one's field of vision and, quite unexpected, appear a few yards away after the observer has been vainly scanning the water in the distance. During calms, when the ocean is silvery, the birds are silhouetted against it and are visible from afar.

Sept. 30. Rainy morning, with lightning; no birds in sight. The weather cleared early, and petrels appeared about nine o'clock. They followed more closely than heretofore, coming under our stern to feed, and even flying forward around the bow. Occasionally I heard them utter a low, rasping note. During the forenoon two of them settled on the water astern and remained there with wings folded for some time. Possibly they were a mated pair affected by the approach of the breeding season.

Oct. 1. None was with us in the morning, but four birds accompanied our whaleboats back to the brig, after the boats had pursued a distant school of sperm whales. The petrels then remained near us for the remainder of the day. Sometimes, when flying low, they would strike backward against the water a dozen times or more with both feet.

Oct. 7. A dark day, with brisk, southwesterly winds and frequent

¹ This also raises the moot question of the source of the name "petrel," which was informally discussed at the November, 1917, meeting of the American Ornithologists' Union. In the present spelling, Dampier's use of the word constitutes its first printed appearance in any language (cf. Murray's Engl. Dict.). Flawes, however, in his Account of a Voyage to Nova Zembla, 1676 (Vol. I, 1694, p. 181) reports that he "Saw many Pitterals about the Ship." This earliest orthography suggests that the name may be derived from the fact that birds of the group "pitter-patter" on the water, which is just what *Oceanites* does. The spellings "petrel" and "peterel" were perhaps made *à posteriori* to fit the popular tradition that Dampier cites.

showers. Wilson's petrels have been with us daily since Sept. 29, but now they are present in legions. We are followed by a veritable cloud of them, and they come so near that, as I sit in the whaleboat lashed across the *Daisy's* stern, I can almost touch some of them with my hand. They skip along the surface as they approach, giving a vigorous kick on the lee side with both feet whenever they touch the water. When they "stand" to feed, the wings are held rigidly and they face the wind; the potential momentum necessary to keep them from being blown away is furnished by the webs, the legs sinking to the heel as they work backward in unison.

Usually silent, they have peeped and chattered considerably to-day — sounds not unlike those made by a nestful of young chickadees when the parent arrives with food. I have been feeding the petrels small bits of pork fat, upon which they swoop voraciously, making a graceful rise to check their course before alighting, and then kicking spray over one another in their eagerness to secure the unusual dainties. I purposely cut off several pieces of fat too large for the birds to swallow readily, and the petrel that captured one would be pursued by his complaining fellows, who besieged him whenever he stood over his tidbit and tried to bolt it. One piece of fat that I cast over had so much of the heavy skin attached that it sank. Three or four petrels had gathered as it fell, but the food was a foot under water before they reached the spot. While I was preparing to throw over another piece without rind, I was astonished to see several birds bob up from the depths, one of them holding the sunken morsel in its bill. Upon experimenting further, I found that they dived most skilfully to a depth of several times their length, leaping forth dry and light-winged from the water into the air.

Apparently the diving powers of some species of Mother Carey's chicken have been noted before, for Newman, in 'Montagu's Dictionary of British Birds' argues circumstantially to the contrary. "We believe," he writes, "the assertion that this bird is expert in diving to be without foundation; the form and levity, too (from having a large proportion of feather, like the Gulls), should alike render them incapable of immersion. They have not the form for pursuing their prey under water, nor do they appear to possess the means of diving; it is from the surface of the sea that they collect their sustenance." All of which shows how far astray deductive reasoning may lead the unwary.

Oct. 8. By 8:30 A.M., four or five of *Oceanites* had gathered in our wake. The numbers soon increased to several dozen, which remained through the day. The water was rather choppy, and the petrels did not skip from crest to crest of the waves, but followed the swell, and pattered in the troughs as much as on the tops.

Instead of wearying toward the close of their day-long flight, they became doubly active about sunset. For the most part they ceased to hunt for food; instead they dashed hither and thither, ecstatically shooting upward almost as high as the mast, then plunging down at great speed, passing often within a yard of my head, as barn swallows do about their nests. I have little doubt that this extraordinary exuberance was correlated with physiological changes due to the near approach of the breeding season.

About six o'clock they deserted the brig for a few minutes in order to flit about a school of jumping skip-jacks (*Carangidæ*), showing that they were still interested in satisfying their appetites. They accompanied us until after dark; I made out the last one just before seven o'clock.

Oct. 9. The petrels took a half holiday. They were plentiful during the morning, but we saw none after noon.

Oct. 10. On this never to be forgotten day, when for nine hours I toiled in a thirty-foot New Bedford whaleboat "fast" to a harpooned and extraordinarily active sperm whale, a whimsical incident occurred. Many Wilson's petrels were feeding over the same area of ocean with numbers of whales. While we were in the midst of a school of whales, it chanced that a petrel dropped to the water to dance and feed just as a whale rose to breathe. The whale shot up suddenly, and the bird, pattering on the sea, happened to be at the precise spot where the whale's blowhole broke the surface. The petrel was literally blown from the nostril of the leviathan and was projected several feet into the air by the blast of steaming breath.

On Oct. 14, 1912, the *Daisy* crossed the equator in longitude 28° W. My observations on the migrant *Oceanites* in the southern hemisphere have already been published in a general ornithological diary in *The Auk* (1914). From the latter article a number of the following notes are drawn.

Oct. 17. A small flock of *Oceanites* followed us in a rather desultory fashion. They did not approach near to the stern. These birds seem to gain confidence with numbers, for when in large flocks they often fly very close. In general, the rougher the sea the more petrels we have about us and the closer they fly to the ship.

Often, as they patter along for some distance on set, slightly depressed wings, they resemble small scurrying quadrupeds. When flying rapidly, and suddenly perceiving food, they sometimes stop their headway by flopping down as though wounded and striking their breasts upon the surface of the water. Perhaps it is this habit which gave rise to the old tradition that the smaller petrels obtain part of their sustenance by skimming the water with the feathers of the breast, and so collecting the oily surface film. Mudie, in 'The Feathered Tribes of the British Islands' (1844), writes that the storm petrels "dash along until they have loaded their

feathers, and then they pause upon the wave and remove the oil with their bills."

Nov. 3. Strong, southwesterly winds, swinging by west towards the north and increasing in violence throughout the day. In the stiff breeze I noticed that the Wilson's petrels always *faced* the wind, diagonally if not directly, with extended, motionless wings, whenever they pattered upon the water. During the afternoon we were running before the wind, and the pursuing birds always wheeled and turned away from our stern before descending to feed. While they were flying with the wind, on the other hand, they kept quite clear of the water.

The greatest numbers of *Oceanites* observed at any time during the entire voyage were seen Nov. 9, in latitude $36^{\circ} 46'$ S., and Nov. 18, in $48^{\circ} 39'$ S. The first date was during relatively calm weather; the second was marked by a terrific southwesterly gale. During both of these days the Wilson's petrels about the ship numbered thousands.

My reasons for believing that identical individuals of this species sometimes followed our vessel for periods aggregating many days, are mainly those of analogy. I have already recorded (*Birds of the South Atlantic*, 1914) how two groups of sooty albatrosses (*Phœbetría*), one of them including a bird which had a readily recognizable peculiarity of plumage, followed our whaleship for four or more days at a time. Single birds of smaller species often associated with the flocks of *Oceanites* in our wake. On Nov. 4, in latitude $33^{\circ} 28'$ S., an example of *Fregetta grallaria* joined the Wilson's petrels. From that date until Nov. 19, in latitude 50° S., I saw never more than one bird of this species, but for periods as long as three days continuously one was always within sight. Therefore I am strongly inclined toward the belief that the *Fregetta* noted at such times was indeed one identical individual, and that the flock of *Oceanites* with which it consorted was likewise composed mostly of the same birds day after day.

Although Wilson's petrels followed us northward from South Georgia, March 15 to May 8, 1913, as may be seen from the entries in the table of records, I made few new observations on the habits of the birds. During a calm on April 19, just south of the equator, I lowered a dory and collected a small series. By throwing grease on the water I attracted many of the petrels close to my boat, and I noticed that two or more of them were one-legged. In Long Island waters I have also seen Wilson's petrels minus a leg, and Mr. Cleaves has observed others during his motion picture work in New York Harbor. Such birds seem to be not in the least incapacitated.

Mr. Beck secured his series at Bahia, latitude 13° S., in approximately the same season as that of my last pelagic collecting. He had come to that

city from Rio Janeiro at the end of February, before the migration period of Wilson's petrel, and had not seen a single bird on the trip; but from April 15 to May 1, 1916 he found them plentiful off Bahia, feeding in the tidal streaks from a half mile to ten miles offshore, flying about independently rather than flocking, and often resting on the water during the calm mid-day. The birds that he collected were, as previously noted, all juvenals, which are doubtless more given to sitting on the water than are the adults.

The fact that all of Allen and Dexter's birds (Mus. Comp. Zool.), collected at Rio Janeiro in May, as well as the single June specimen from the African coast, are likewise juvenals, whereas all my spring specimens taken far offshore are fully adult, suggests that the young of *Oceanites* may follow the coast-lines of the southern continents during their first northward migration. This hypothesis would account for the apparent segregation as regards age, and would not be out of harmony with known facts in the life history of many other species of birds. That the adults, on the other hand, do not preferably migrate along the conformation of land masses is known from abundant data, of which the records in this paper are a part. The naturalists of the *Scotia* (Clarke, 1913a) found the species in numbers in the vicinity of Gough Island, south of the Tristan Group, in April 1904, the season of northward migration. This locality lies about as far from a continent as it is possible to go in the South Atlantic.

Where the majority of the young spend the first northern summer is not known. Certainly they constitute only a small fraction of the birds occurring along the coast of the eastern United States; otherwise the series of skins in American ornithological collections would not consist so overwhelmingly of adults. The juvenal specimen which was taken off the equatorial African coast on June 20 shows that not all the young birds pass across the tropics, even though examples have been obtained as far north as Newfoundland.

Of equal uncertainty is the whereabouts of the first-year birds during the northern winter, or breeding season. The fact that the young undergo no molt until after they have left the coast of the United States, and probably not until their second summer, tends to confirm an inference drawn from examination of breeding birds from South Georgia, namely, that the yearlings do not breed. Perhaps, therefore, they spend their entire first year at sea, a supposition which would explain the occurrence of *Oceanites* in the tropical Atlantic during November (cf. Salvin, 1896) and other winter months.

As regards the adults of *Oceanites*, the meager facts available indicate that all, or most of them, penetrate far into the North Temperate Atlantic during the summer months, and spend the lull between the ebb and flow of the long migration chiefly in the western part of that ocean, between the

latitudes of Bermuda and Greenland. It is surely significant that I saw no examples of so widespread and conspicuous a bird, during the *Daisy's* long transatlantic cruise, south of the thirtieth parallel of north latitude in the months of July, August, and part of September, especially as my experience is in accord with the observations and conclusions of other naturalists, notably Dr. Glover M. Allen and Mr. John Treadwell Nichols. The former authority (1905) writes of birds of this species seen during a voyage to the Bahamas:

Petrels were seen from the first morning out of New York [June 24, 1904] until we had crossed the Gulf Stream off Hatteras. During this time large flocks of from thirty to fifty birds were occasionally seen, while a few were almost constantly observed flying zig-zag back and forth over the steamer's wake some hundred yards or more astern. After entering upon the Gulf Stream and the warmer waters to the south, only one or two single birds were seen, the last being in about lat. 28° N. Cory, while cruising among the Bahamas at an earlier time of the year, found petrels abundant at a short distance off the coast, which might indicate that the birds were at that time passing through the latitude of the Bahamas and by July, when we made our trip, the main flight had passed still farther to the northward. On our return voyage, July 28-31, the first petrels, three or four in number, were observed after crossing the Gulf Stream off Hatteras Light, but they did not become common until we were within some 300 or 400 miles of Sandy Hook.

Mr. Nichols has kindly supplied me with the following note in manuscript:

In the western North Atlantic in summer the Wilson's petrel seems to occur on the continental shelf, and out across the Gulf Stream to its eastern edge, and to be little more than a straggler further east on the deep, currentless, central area. It thus is not common about Bermuda.

In August 1906, sailing E. S. E. from New York, it was constantly present to about lat. 38° N., long. 68° W. (Aug. 10), where the last few birds were seen. On the previous day, in 40° N., and 70° W., they had been common and the following day, in 38° N., 64° W., they were gone. Again, in 1914, crossing the Gulf Stream diagonally S. S. E., at a time when the species was common in New York Harbor, a few were seen as far out as about 35° N. 72° W. (July 5) and none further. Returning later over the same course we picked them up at about 37° N., $72^{\circ} 30'$ W. (Aug. 9). In 1909, bound east, Mother Carey's chickens, which I have every reason to believe were this species, were common at about 41° N., 55° W. (May 14), and few, if any, were seen further east.

The species is known to be rather rare in the vicinity of the British Isles, while it is abundant in midsummer in the Gulf of St. Lawrence, on the Grand Banks, and along the Labrador coast. It has been recorded from Hudson's Strait in September, and it is likely that some birds wander northward into Baffin's Bay. If so, the pelagic range extends as far north of the equator as the breeding grounds lie south of it.

NOTES ON THE BREEDING OCEANITES OF SOUTH GEORGIA

Lönnerberg (1906) records, on the authority of Sörling's observations, that Wilson's petrel occurs at South Georgia during all of the southern summer, disappearing about the end of March. The birds had not yet returned when Sörling departed from the island early in October 1905. The dates of arrival and departure for the South Orkneys, seven degrees of latitude farther south, are given by Clarke (1913) as Nov. 11 and March 23, respectively.

The *Daisy* reached South Georgia on Nov. 23, 1912, at which time *Oceanites* was already common in the fiords, and enormously abundant on the whaling banks forty miles offshore. On Dec. 1, just at dusk, great flocks were seen feeding in King Edward Cove, Cumberland Bay. Thereafter we found them in the bays wherever we went and, although I failed, in spite of patient search, to discover a nest, many of the birds shot were undoubtedly "hot off the egg," having bare brood-patches in addition to enlarged testes or ovaries.

At the Bay of Isles, near the northwestern end of South Georgia, the crew of the *Daisy* engaged extensively in sea elephant hunting, with the result that quantities of blubber lay soaking in the water alongside the vessel much of the time. This attracted flocks of *Oceanites*, especially during gales, when groups estimated to comprise as many as six hundred birds often foraged for globules of oil washed out of the soaking blubber.

Over the headlands and tussock flats along the Bay of Isles, the birds were frequently seen flying back and forth like martins, but I never spied one in the act of alighting at its nesting site. On the morning of Feb. 1, I watched a single bird for a quarter of an hour while it dashed to and fro and up and down before a steep, rocky bank near the bay. It flew precisely as though it were hawking winged insects, which was, of course, very unlikely. For several minutes it was chased in all its gyrations by a pipit (*Anthus antarcticus*), the latter trying vainly to keep close behind it. Finally it flew off without disclosing the nesting site, if indeed it were in the neighborhood.

A most interesting point about *Oceanites* at South Georgia is a fact of an ecologic nature, namely, that this species, practically alone among the smaller water birds, enjoys absolute immunity from the aggressiveness of the skua (*Catharacta*). Lönnerberg has recorded this before but my observations of the actual conditions were none the less a source of considerable surprise to me. The skua is to most of the birds, large or small, a wanton and relentless ogre. It is forever watching for neglected young of pen-

guins, cormorants, and even albatrosses; it attacks at sight the endemic teal, the diving petrel, and the *Prion*. To the last two species, it is such a terrible foe that they dare not show themselves in the fiords or over the land between daylight and dark; nevertheless, the skuas succeed in capturing so many of them that their dismembered carcasses strew the ground over their subterranean colonies. But *Oceanites* flies about with impunity in broad daylight. I have seen one almost brush a skua with its wing as the latter bird stood on a rock in the kelp fields, and both species sometimes fed together when stormy weather had washed away pieces of seal blubber from the supply floating alongside our brig.

Why does the skua ignore this petrel? It is surely as conspicuous as the diver (*Pelecanoides*) and seemingly less difficult to capture than the fleet-winged *Prion*. The protective character cannot be in an offensive taste, for the skua is quite ready to pounce upon and devour a dead or disabled *Oceanites*. Possibly, however, its body affords too small a morsel to warrant any effort on the skua's part. It is noteworthy that the latter grants a like immunity to one other still smaller bird, the pipit (*Anthus*).

Wilson's petrels were present in apparently undiminished numbers when we left South Georgia on March 15, 1913. As the *Daisy* stood to sea from Possession Bay, I had occasion to make a trip in a whaleboat to a neighboring whaling station for the purpose of posting mail. Shortly after sunset we started on a ten-mile pull to the brig offshore, and, as soon as we were well out from the land, our boat was continually in the midst of innumerable small Tubinares flocking over the quiet sea. *Oceanites* made up a considerable proportion of these birds, which fluttered all about us. Their indistinct forms kept flashing above the skyline, but their myriad numbers were revealed still more by a chorus of twitterings and the soft unbroken sound of winnowing quills.

At this season the northward migration had commenced, for, as related above, the petrels accompanied the *Daisy* on her voyage towards home.

NOTES ON SUMMER VISITANTS NEAR NEW YORK

Wilson's petrels are variably common in the Lower Bay of New York and in the waters about Long Island, including the Sound, from early May until September. Their presence close inshore is very irregular, but in August 1907, for instance, they entered New York Harbor in conspicuous numbers and during the first week of August 1915, when they were notoriously abundant at many points near New York, Chapman (1916) saw twenty or more in the Hudson River opposite 130th Street. Earlier in the

same summer, I had noticed numbers of them near the western end of Long Island Sound. On Aug. 18, 1916, I saw one feeding in the Great South Bay off Babylon, Long Island. At other times I have seen birds fly into the inlet of Jamaica Bay, and several observers have reported them inside Fire Island Inlet (cf. Nichols, Murphy, and Griscom, 1917). In June and July their molted flight feathers, recognizable from the persistent Tubinarine odor no less than from their appearance, are often much in evidence along the drift-lines of the south shore of Long Island.

On Aug. 4, 1915, I witnessed a remarkable flight on the south coast, near Montauk Point. A heavy, southeasterly storm, with much rain, had raged all morning of this day. During the afternoon the wind veered to the south, and a huge surf battered the coast in many lines of breakers. At four o'clock, Mr. Francis Harper and I saw an interminable line of Wilson's petrels flying eastward near shore, skimming along the troughs in the midst of curling waves. They frequently stopped to feed, and some of them flew within sixty yards of the beach. We shot three that came within range while we stood with the surge washing over our feet, and the wind quickly whisked their bodies ashore. The stream of petrels, all making towards the east, extended offshore as far as we could see; at times scores of them must have been passing us every minute. By five o'clock, the main body of this flight had gone by, for thereafter we saw only a few stragglers.

The three birds collected on this occasion were rather thin, unlike the plump specimens taken at South Georgian breeding grounds. The testes of the two males were minute and slightly pigmented.

Four days later, Aug. 8, we collected additional specimens from a launch off Montauk Point, and found that the petrels were utterly indifferent to the report of a gun and that it was easy to decoy them within camera range by allowing the dead bodies of two or three to float upon the water.

FOOD OF OCEANITES

Statements regarding the food of the smaller petrels have usually been of a very general nature. The fact that these birds eat oil and fat wherever they are available is no indication that they rely upon, or often find, such substances on the open ocean. Wilson's petrel is, of course, readily attracted around a boat by oil, grease, or ground fish thrown on the water, and Mr. Cleaves used cod-liver oil as bait in obtaining some of his unusual photographs. I have seen them feed upon putrescent fish and the fly maggots washed out of it. Usually they deal with food in small particles, but I have

watched a bird in New York Bay feeding upon a large chunk of refuse — “standing” on the water, with quivering wings held high, while it tugged and pulled at the food as a robin might pull at a worm.

Stomachs examined at South Georgia contained chiefly blubber or scraps from the whaling stations or sealing vessels, food supplies produced, therefore, through the agency of man. The birds have been seen, however, feeding in flocks about the carcass of a dead whale at sea, picking up small bits of carrion dropped from the beaks of *Macronectes* and other large species. Long Island birds that I have dissected have had only greenish slime in their stomachs, and the label of a one-legged Long Island specimen in the American Museum Collection states “Contents of stomach very fine sea weed, green and grass-like.”

At sea, Wilson’s petrels profit by the destructive work of schools of predaceous fish, as noted in my narrative. Probably this habit accounts for the frequent loss of a leg; a barracuta might readily snip off one or both feet while a petrel was engaged in gathering scraps from the slaughter. Birds that lose both feet never live to tell the tale, but some of those less seriously maimed evidently recover.

The stomach contents of three Wilson’s petrels collected south of the Cape Verdes in September 1912, consists of six otoliths of small fishes, a large assortment of crystalline lenses apparently from the eyes of small fishes, traces of algæ and minute crustaceans, some cinders of volcanic ash, and what appear to be Dipterid eggs. The last may have been laid upon the stomachs on shipboard after they had been removed from the bodies. Probably such small forms of life as make up the remainder of this list constitute the bulk of the petrels’ food during their pelagic wanderings.

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Fig. 1. *Oceanites* hovering above the water, Lower Bay of New York, Aug. 9, 1914.



Fig. 2. *Oceanites*, Lower Bay of New York, early August, 1915. At least two of this trio have completed the molt of the remiges. In the petrel at the left, the new quills have not yet grown to normal proportions.

Both photographs by Howard H. Cleaves





A flock of *Occanites* attracted by the "chum" (ground menhaden) of a blue-fisherman, New York Bay, early August, 1915. The bird in the background is carrying a piece of fish in its bill. Photograph by Howard H. Cleaves.



A flock of *Oceanites* skipping along the surface of New York Bay, Aug. 9, 1914. Photograph by Howard H. Cleaves.

**Article V.—LIFE HISTORIES OF NORTH AMERICAN SPECIES
OF THE GENUS *CATOCALA***

BY WM. BARNES, M. D. AND J. McDUNNOUGH, PH. D.

In anticipation of the forthcoming 'Illustrations of the North American Species of the Genus *Catocala*' to be published shortly as one of the Memoirs of The American Museum of Natural History, we offer the following notes on the early stages of a number of species of *Catocala*. These notes are the outcome of extensive breeding experiments carried on by us during several seasons and, for the most part, deal with species of which the early stages were either partially or totally unknown; in a few instances we have amplified, for reasons stated in the text, existing descriptions. Figures of the mature larvæ, as well as enlarged drawings of the head and certain body segments of nearly all the species included here, will be published in connection with the above mentioned Memoir.

We take this opportunity of expressing our thanks to the numerous correspondents who have materially aided us in securing ova of the various species.

***Catocala innubens* Guenée**

OVUM.—Rather more than hemispherical; strongly ribbed vertically with about 35 to 40 ribs, half of which attain the micropylar area which is sharply defined by an encircling raised rim, the remaining ribs arising interspaceally at the equatorial zone and usually unbranched; micropyle slightly raised and separated from rim by a faint depression; numerous faint transverse ribs; base flat; color gray. Diameter, 1 mm.

LARVA.—*Stage I*.—Head pale whitish, with brown vertical stripe. Body whitish, with three brown lateral stripes and a fourth subspiracular stripe; on the first four abdominal segments tubercle V has a brown dash behind it, which is possibly an incipient fifth stripe. Length, 3 mm.

FOOD-PLANT.—Honey locust (*Gleditschia triacanthos*).

A description of the remaining stages is given by G. H. French in Can. Ent., XX, p. 170; further notes on the larva are recorded by R. R. Rowley in Ent. News, XXI, p. 107.

Our own observations on the larval stages showed only three molts, but we imagine we must have overlooked one of the early ones, as four molts is the minimum number we have met with in any other *Catocala* larvæ.

Catocala piatrix Grote

OVUM.—Hemispherical; strongly ribbed vertically with about 35 ribs, about half of which reach to just before the micropylar area; the remainder arising interspaceally in the equatorial zone and scarcely ever branching; micropyle surrounded by a raised rim and consisting of very minute cells; base flat; color liver-brown. Diameter, .9 mm.

LARVA.—*Stage I*.—Head yellowish. Body pale yellow-green, with black tubercles and three brown lateral stripes, the lower of which is much broken.

Stage II.—Head white, lined longitudinally with black-brown. Body pale olive-brown, with pale geminate dorsal line and three similar lateral ones.

Stage III.—Head whitish, lined rather variably with black and red-brown, the latter color predominant at apex and on cheeks. Body pale gray-green, tinged below tubercle III with blackish; a pale geminate dorsal stripe bordered faintly with black and coalescing on prothorax and rear abdominal segment; two lateral stripes above tubercle III and a third one below this tubercle, all bordered with black lines; beneath yellow-green, with black patches. Legs pale orange.

Stage IV.—Similar to preceding stage but lateral black area more prominent and border lines to stripes very clear and marked.

Stage V.—Head reddish, streaked with brown except for a white vertical streak in front. Body as before but stripes are more or less merged in the ground color and the dark border lines are the most prominent feature; each pale stripe shows a faint dark dotted central line.

Stage VI.—Head either unicolorous red or heavily shaded with black apically and laterally. Body pale greenish-gray, shaded laterally with blackish, without warts or lateral filaments; tubercles small, whitish. The border lines of the previous stage still persist but are broken up into numerous dots and not very prominent. Length, full-grown, 70 to 80 mm.

FOOD-PLANTS.—Walnut, hickory, and butternut.

The description given by G. M. and E. A. Dodge of the mature larva in Can. Ent., XXXIII, p. 299, differs so much from our own observations, especially in the very characteristic color of the head, that we have grave doubts as to the correctness of the authors' identification of the larva. Mr. R. R. Rowley (Ent. News, XX, pp. 13, 133) records an amount of variation in the larva far greater than any we have remarked although we have bred the species several years in succession from ova laid by captured females and also from those collected under hickory bark; the matter will require further investigation.

Catocala epione Drury

OVUM.—Rather more than hemispherical, quite different from any of the known ova of the black-winged forms; micropyle composed of about twenty-five minute cells encircled by two rather irregular rows of slightly larger cells; from this area about nineteen ribs arise and run vertically to base of egg, being augmented by about nineteen others arising slightly below the point of origin of the first group; these are crossed by numerous faint transverse ribs; base flat; color grayish. Diameter, 1.4 mm.

LARVA.—*Stage I*.—Pale gray with three lateral red-brown lines and a fourth subventral one; tubercles black with rather long setæ. Head reddish, frontally gray. Much larger than is usual among hickory-feeders, resembling in this respect one of the oak-feeders. Length, 3 to 4 mm.

Stage II.—Head whitish, with two longitudinal geminate black lines, the inner one being slightly curved. Body pale purplish gray, with three white lateral stripes and a geminate dorsal one slightly widening on the abdominal segments into the characteristic diamond patches; tubercles small, black.

Stage III.—Head pale, longitudinally lined with black with slight open V above the apex of clypeus. Body pale powdery gray, with the stripes as in the preceding stage but each one bordered on both sides by a dark line; the stripes themselves are only slightly paler than the ground color.

Stage IV.—Head pale flesh-color, longitudinally lined with black, the lateral striations uniting to form a more or less geminate black border to the lobes. Body light gray, very powdery; markings essentially as before, but the pale stripes are almost merged in the ground color and the black border lines stand out correspondingly more distinctly, giving the general appearance of geminate dorsal black lines and seven lateral lines of which the first is just above tubercle II, the second below same, the third and fourth between tubercles II and III, the fifth crossing tubercle III, the sixth spiracular, and the seventh crossing tubercle V; posterior portion of each segment tinged with ochreous in the position of the stripes of earlier stages; no filaments, tubercles small, slightly ochreous; beneath with purple-black patches. Prolegs pinkish, lined laterally with black.

Stage V.—Head pale umber brown, deeper apically, with broad black encircling band, curved forward somewhat between the apices of the lobes; frontally with longitudinal brown lines. Body cylindrical, without humps or filaments; whitish gray, powdery; the lines of the preceding stage are broken into dark spots and between them secondary dark spots occur forming a rather evident subdorsal dark stripe which accentuates the pale

centrodorsal diamond stripe, and two less-marked lateral stripes; in the areas representing the pale stripes of former stages the dark spotting is paler than in the interspaceal areas. Legs pale umber; prolegs tinged with pinkish-brown and bordered posteriorly by a stripe of similar color. Length, 45–50 mm.

FOOD-PLANTS.— Various kinds of hickory (*Hickoria* spp.). The record of oak as a food-plant (Wormsbacher. Zeitsch. Wiss. Ins. Biol., VIII, 1912, p. 257) is probably erroneous.

Catocala habilis Grote

OVUM.— Belongs in the same group with *residua*, *neogama*, etc., being flat, circular, with saucer-shaped base and raised rim around point of greatest diameter; micropylar area consisting of about 45 small, hexagonal cells; radial ribs well marked, numbering about 30 at the rim and 12–14 at micropyle; transverse ribbing distinct; color brown. Diameter, 1 mm.

LARVA.— *Stage I*.— Head brown, flat. Body green-gray, with three broad reddish lateral stripes; tubercles and setæ, black.

Stage II.— Head black. Body with dorsal area purple-gray and lateral area deep purple crossed by two whitish lines.

Stage III.— Head black, slightly streaked with white frontally. Body blackish, with geminate pale dorsal line, two pale lateral lines above spiracle, and a third one below same; beneath whitish.

Stage IV.— Head flat; whitish, heavily lined with black of which the most prominent feature is an open V mark, heaviest across the apices of the lobes and descending as a thin line along the sides of the clypeus to the mouth. Body rather shiny blackish, with pale geminate dorsal line, the two component parts not coalescing or only very slightly so; three pale lateral lines.

Stage V.— Much as before but head blacker. Body smooth shiny black, marbled with whitish; dorsal and lateral stripes as before, the lowest one slightly yellowish; tubercles black, except tubercle V which is tinted with orange; no filaments; beneath greenish white. Legs pale.

Stage VI.— Head flat, whitish, heavily marked with black laterally, so that entire lateral portion is often completely shiny black; frontally a sort of W mark is evident. Body shiny, deep black-brown, marbled with whitish; dorsal geminate line fairly distinct; dorsal tubercles orange; lateral pale stripes I and II obscure but present, with further white marbling interspaceally; a rather distinct dark spiracular band is present due to increase in the dark marbling; below the spiracle stripe III is distinctly

yellow-orange with tubercles V and VI also bright orange; this entire region is heavily mottled with brownish; lateral tubercles small, blackish; no filaments. Legs pale-brown; prolegs still paler brown.

Stage VII.—Head flat, pale, with broad blackish lateral band, broadening at mouth, a dark patch at the posterior portion of the suture dividing the two lobes and a reddish brown or blackish line crossing the apices and breaking up below them into streaks which descend irregularly towards the mouth. Body, in general appearance, deep black-brown, due to heavy dotting over a pale ochre ground color; pale dorsal geminate line broadening out slightly at the rear of each segment; two pale lateral lines very indistinct except on thoracic segments; a dark spiracular band below which the mottling is distinctly lighter brown with stripe III rather more yellowish and also mottled; legs pinkish-brown; tubercles ochreous, V and VI being tinged with orange, setæ short, white; no filaments; beneath greenish white with the usual dark blotches. Length, 50 mm.

FOOD-PLANT.—Hickory.

Seven stages is rather remarkable for a *Catocala* larva and is only, so far as we know, equalled by *vidua*; our notes are verified by preserved material before us.

The mature larva has been described by both Dodge (Can. Ent., XXXIII, 1901, p. 276) and Rowley (Ent. News, XX, 1909, p. 134).

Catocala robinsoni Grote

In 1913 we bred a series of the form *curvata* from a batch of flat ova, laid in overlapping rows, found beneath the bark of a shell-bark hickory. Unfortunately, other work prevented us from obtaining a detailed description of any of the various stages except the final one which is as follows.

LARVA.—Head flat frontally, lobes rounded apically, pale gray with a heavy black lateral border to each lobe continued and joined behind the apices; frontal portion slightly marbled with purple-brown forming an inverted V mark in the region of the clypeal apex. Body pale fleshy-brown, mottled with dark dots; the dorsal diamond patches are followed by a more or less prominent subdorsal dark band edged with a distinct dark line; a blackish spiracular band; tubercles minute, black, arising from a creamy base; no humps or lateral filaments; spiracles smoky with black rim. Length, 60 mm.

FOOD-PLANT.—Hickory.

It is apparent from the above description that the larva is closely related to that of *residua* but still more so to that of *habilis*.

Catocala residua Grote

OVUM.—Very flat; base slightly convex; the sides rising to a rather pronounced rim which encircles the egg at the point of its greatest diameter. The surface of the egg from this rim to the micropylar area, which is only slightly raised above the plane of the rim, is strongly ribbed; about 35 to 40 ribs radiate inward towards the micropyle from the rim but only a small proportion actually attain the micropylar area; these strong radial ribs are crossed by numerous minute transverse ones forming a network on the whole upper surface, the meshes of which increase in width as they approach the outer rim; micropyle composed of numerous minute cells; color olive-brown. Diameter, 1 mm.

LARVA.—*Stage I*.—Head blackish-brown. Body pale whitish gray, with three reddish-brown lateral stripes, equidistant, the first on a level with tubercles I and II (dorsal tubercles); a fourth similar subspiracular stripe rather broken and indistinct; tubercles black with short setæ.

Stage II.—Head black, shaded with white. Body purple-gray with geminate white dorsal line enclosing the customary diamond-shaped dorsal patches which are rather elongate; three distinct white lateral lines; tubercles black; ventrally paler.

Stage III.—Head white, streaked longitudinally with black forming an open V frontally above the clypeus. Body brown-gray; a geminate pale dorsal stripe bordered by dark lines, irregular in course, joining in the centre of each segment and thus forming dorsal diamond patches with dark centers which are formed by the inner dark border lines partially coalescing; three pale lateral stripes as in preceding stage, but now bordered by dark lines.

Stage IV.—Head whitish, striped longitudinally with black, the most prominent stripe descending from the prothorax over the apex of each lobe to about the level of the point of the clypeus where it branches; a stripe of almost equal thickness ascends from the base of the palpi about half the height of the lobe; the clypeus has a central dark streak. Body whitish, slightly ochreous dorsally, especially toward rear of segments; dorsal tubercles slightly orange-tinged. The stripes of the preceding stage with their dark border lines are still present but are not so distinct, being only slightly more ochreous than the general ground color; the dark border lines on the contrary are very prominent so that the general appearance is that of an ochreous gray larva with a broken dorsal brown line, a waved subdorsal one above tubercle II, and six brown lateral lines; lateral tubercles black; no lateral filaments.

Stage V.— Head grayish, streaked with black much as before; the heavy dark stripe over apices of lobes has assumed an orange tint; the one above the palpi is still dark and heavy. Body gray-brown, rather smooth, with no dorsal warts or humps; tubercles orange. General appearance much as in preceding stage. The pale stripes have been practically absorbed into the general ground color; the dark lines show a tendency to break up into numerous spots and are bordered on each side by a fine white line. Between the dark lines, in the areas forming the interspaces between the white stripes of previous stages, there is a tendency for secondary dark spots to appear, especially in spiracular region where a more or less prominent dark spiracular band is thus formed; no lateral filaments; beneath whitish. Legs pale ochreous.

Stage VI.— Head whitish, with prominent angled black streak above the palpi reaching only slightly above the region of the ocelli; numerous vertical brown lines joined in a fine brown network, the most prominent of which is a vertical streak across the apex of each lobe. Body smooth, pale gray, with a slight whitish bloom. Appearance much as before. The secondary dark dots have become very numerous forming more or less prominent subdorsal and spiracular dark bands; tubercles orange-yellow; no filaments. Prolegs whitish with lateral black streak. Length, 50 to 60 mm.

FOOD-PLANT.— Hickory.

The full-grown larvæ are very similar to those of *retecta*, but may at once be distinguished by the entire absence of lateral filaments. We succeeded in rearing a good series of this species from ova received from Mr. R. R. Rowley of Louisiana, Missouri. The resulting imagines were all typical *residua* in the contrasting maculation of primaries and the brown fringes of secondaries. A single ovum received from Mr. Reiff of Boston as *obscura* showed no difference as a larva and produced an imago with primaries entirely similar to those of our Missouri series, but having the fringes of secondaries slightly tinged with white at their extreme apex. A single one of our bred Missouri specimens showed a similar coloration. We should not be surprised if *residua* with entirely white fringes on secondaries might occur.

Catocala retecta Grote

Prof. French has given a very complete account of the ovum and larva of this species (Can. Ent., XXVI, 1894, p. 97) in which he records six larval molts.

We have bred this species in large numbers from ova received from R. R. Rowley of Louisiana, Missouri, and also from Miss Berry of Vinton, Iowa.

We observed only six larval stages (i. e. five molts) and preserved material of all these stages before us seems to verify this conclusion. We think that Prof. French described an advanced stage of the first larval instar as "after first moult." We append brief notes on the stages, as noted by us, which will serve to amplify in certain directions Prof. French's excellent description.

LARVA.—*Stage I.*—Head black-brown. Body gray with three lateral brown lines; tubercles black.

Stage II.—Head black, lined with white frontally. Body purple-black with geminate dorsal white line and three lateral ones.

Stage III.—Resembles greatly the larva of *C. residua*. Head white, heavily lined vertically with black, with open V mark above clypeus. Body blackish, with geminate pale dorsal stripe bordered with brown line and partially coalescing to form diamond patches towards the rear of first four abdominal segments; three pale lateral stripes with similar dark border lines.

Stage IV.—Head white, heavily lined with black. Dorsal and lateral stripes as before, bordered with black and distinctly paler than the ground color. Tubercle I orange, tubercle II usually black. Very similar to *residua* but with lines rather more distinct and the dorsal diamond patches on abdominal segments rather broken.

Stage V.—Head whitish, with black longitudinal stripes and rather heavy purple-red stripe at apex. Body rather dark smoky black, due to heavy black secondary dots on a pale ground; a geminate dorsal stripe forming more or less distinct diamond patches; lateral pale stripes slightly evident, with heavy border lines tending to break up into dots; the interspaces between pale stripes filled with dark dots, tending to form dark subdorsal and spiracular bands; tubercles orange; lateral filaments present, which at once distinguishes the species from *residua*.

Stage VI.—Head flat, lobes rounded, whitish, with numerous longitudinal purplish striations; a heavy black streak from above palpus to below apex of lobe, angled inward in the region of the ocelli; apex with bright brown streak. Body pale, creamy, very heavily sprinkled with black dots and streaks; the pale dorsal diamond patches with centrodorsal black band are fairly distinct; these are bordered by a dark subdorsal band containing the orange dorsal tubercles; laterally the three pale stripes, separated by two black bands may, in a general way, be traced; of these interspaceal dark bands, the spiracular one is broadest and most distinct; the dark bands on the fifth abdominal segment are intensified in color so as to almost give the appearance of a transverse dark band; lateral tubercles pale purplish; filaments whitish. Legs and prolegs pale purplish. Length, 50 mm.

FOOD-PLANTS.—Hickory and walnut.

Catocala vidua Abbot and Smith

Prof. French, in his otherwise very excellent description of the larval stages (Can. Ent., XX, 1883, p. 28), has overlooked one of the early molts, viz., the second. We have bred the species in numbers and found that there were six molts and therefore seven larval stages, and have before us at the present moment, as conclusive evidence, preserved material representing all these stages. The differences between the second and third larval stages are only slight, the latter stage showing the development of dark border lines to the pale lateral stripes.

The ovum is quite similar to that of *resecta* Grote but smaller, being remarkably small for the large size of the imago.

Catocala lacrymosa Guenée

OVUM.—Circular, rather flat, but not nearly so much so as in *residua*; base of egg saucer-shaped, the sides rising almost perpendicularly to a point about one-third the total height of egg, where a very slight rim is formed at the point of the greatest diameter of the egg; from this rim the sides slope gently inwards and upwards to the micropyle, the whole upper surface being thus distinctly convex. From the micropyle, which consists of a rosette of small cells, well defined radial ribs descend to the rim, branching dichotomously shortly below micropyle and numbering, at the rim, about 35. These ribs are continued across the rim down the sides towards the base and are crossed over the whole surface of the egg by numerous fine transverse ribs forming a network of cells which decrease in width towards the micropyle; color purplish-brown. Diameter, 1.1 mm.

LARVA.—*Stage I*.—Head brown. Body pale gray, with black tubercles and three brown lateral lines.

Stage II.—Head rather pale gray streaked with white frontally in lower portion and with prominent black streak, rather inwardly oblique, crossing the apex of each lobe and descending to below apex of clypeus. Body pale gray dorsally with faint geminate dorsal line enclosing an open chain of diamond patches; laterally red-brown with three white lines.

Stage III.—Head pale, striped longitudinally with black; a prominent black stripe descending from the apex of each lobe along the suture to about the level of the apex of clypeus; below this, a white stripe to the mouth parts. Body rather pale gray-brown with geminate pale dorsal stripes and three lateral ones bordered on each side by a brown line; tubercles black, more or less ringed with white basally.

Stage IV.—Head white, lined longitudinally with black with V-shaped mark on each lobe centrally and heavy black vertical dash at apex of lobes; a black streak from base of palpus half way up the cheek. Body whitish, rather variegated with black which tends to form subdorsal patches on the first and second abdominal segments between tubercle II and tubercle I of the following segment. These patches are formed by a suffusion of the lower black border of the dorsal stripe mentioned in the previous stage and the upper one of the first lateral stripe which dark line is very distinct all through its course. The same tendency is shown between the lower border of the second lateral stripe and the upper border of the third one, giving the impression of a broken spiracular dark band. The other border lines are fainter and tend to break up into dots, whilst the stripes themselves are hardly as pronounced as in the previous stage. A slight blackish suffusion extends dorsally across the posterior portion of the fifth abdominal segment and the anterior portion of the sixth. Tubercles more or less tinged with orange, dorsal tubercles on eighth and ninth abdominal segments being conical and prominent. No dorsal hump. Sparse white lateral filaments. Legs and prolegs pale. Length, 25 mm.

From ova received from Mr. R. R. Rowley of Louisiana, Missouri, we were only successful in raising larvæ to this stage on hickory. There are probably still two more stages, at least. The pale, rather variegated appearance and the lateral filaments would point towards association with the *vidua* group.

Catocala neogama Abbot and Smith

OVUM.—Very similar to those of *residua* and *lacrymosa*; flat, circular, the base saucer-shaped with the sides rising to a rather poorly defined rim encircling the egg at about one-half of its height; the upper surface of the egg has its sides sloping gently inward and upward to the micropylar area which consists of numerous, small hexagonal cells, rather larger, however, than usual; the radial ribs are distinct, about 35 to 40 in number, of which about 16 touch the micropylar area; transverse ribbing rather more distinct than in allied species; the ribbing is continued below the rim; color brown. Diameter, 1 mm.

LARVA.—*Stage I.*—Head black-brown. Body pale gray with three brown lateral lines, the lower of which is often broken; tubercles black.

Stage II.—Head black, mottled with white. Body purplish-brown, in early stages rather banded in appearance owing to the segmental incisions being paler; a geminate dorsal line enclosing the usual diamond patches; three pale lateral lines; tubercles black, II being rather large.

Stage III.—Head whitish-ochre streaked with black. Body rather dark black-brown, deepest on first four abdominal segments on each side of the pale geminate dorsal stripe, giving the appearance of a broken dark subdorsal stripe crossing tubercles I and II; first two lateral stripes very closely approached and at times almost confluent, the upper border of the first stripe being very irregular in outline; stripe three as in preceding stage; all pale stripes bordered by a dark line. Legs blackish.

Stage IV.—Head as before, pale ochreous streaked longitudinally with black, a short stripe crossing the apex of each lobe being the heaviest. Body rather pale gray heavily lined with black; pale dorsal diamond patches distinct, rather yellowish, with heavy black lateral shading on the first two abdominal segments filling in the entire interspaceal area to first pale lateral stripe; the posterior portion of the fifth and the anterior portion of the sixth abdominal segments are crossed by a transverse dark ring cut by the pale dorsal stripes; three lateral stripes as before with dark-lined edges; tubercles with slight orange tint.

From ova received from R. R. Rowley of Louisiana, Missouri, we were only successful in rearing larvæ to the above stage; there are probably two more stages, making six in all, as is usual in this group.

FOOD-PLANTS.—Hickory and walnut.

Descriptions of the mature larva have been given by G. M. and E. A. Dodge (Can. Ent., XXXIII, 1901, p. 299) and W. Beutenmüller (Bull. Amer. Mus. Nat. Hist., XV, 1902, p. 385).

***Catocala parta* Guenée**

OVUM.—Hemispherical; micropyle a collection of small cells surrounded by a slight circular raised rim outside of which is a single row of small encircling cells; about eighteen vertical ribs arise from this area, branching rather irregularly after a short distance and producing 35 to 40 ribs toward base of egg; faint cross-ribbing; color brown blotched with yellow. Diameter, 1 mm.

LARVA.—*Stage I.*—Very small when freshly emerged. Head pale brown. Body dirty gray, with three rather broad lateral red-brown stripes; later in the same stage, brown with paler dorsal area and three whitish lateral stripes.

Stage II.—Head pale brown, with narrow black border and slight dark marbling. Body dorsally pale olive, laterally smoky brown; markings very obscure, consisting of three pale lateral stripes margined by darker lines.

Stage III.—Much as in preceding stage. Head with apices of lobes tinged with orange. Body pale olive, with paler dorsal diamond patches and lateral stripes bordered with fine black lines; all maculation very obscure; a small dorsal orange wart on fifth abdominal segment with slight dark lateral shade below it.

Stage IV.—Head flat; flesh-color, mottled with pale purplish, with orange apex and strong black lateral border. Body pale brown, with paler geminate dorsal stripe forming the usual diamond patches; three lateral pale stripes, bordered with black lines, with subdorsal interspaces often darker, giving the appearance of a broken dark subdorsal band; small ochreous transverse dorsal wart on fifth abdominal segment with mere suggestion of a dark lateral shade but with interspaceal dark stripes rather prominent in this region; tubercles orange. Resembles greatly, in this stage, the full-grown larva of *irene*.

Stage V.—Practically as before; dark bands in interspaces between pale stripes rather better defined; transverse wart larger, extending laterally to tubercle II; on eighth abdominal segment, tubercle II conical and prominent. Length, 40 mm.

FOOD-PLANT.—Willow.

The above notes were made from ova laid by a female from Utah; we were unsuccessful in bringing the larva to maturity. There is probably one more larval stage before pupation.

The mature larva has been described by W. Beutenmüller (Bull. Amer. Mus. Nat. Hist., XVI, 1902, p. 387).

Catocala luciana Strecker

OVUM.—Similar to that of *C. briseis* and its allies.

LARVA.—*Stage I.*—Similar to those of allied species. Head reddish. Body dark, dirty green, gradually paling during growth; lateral area purplish brown, crossed by three parallel lines of the ground color; beneath pale greenish.

Stage II.—Head whitish, streaked with brown on cheeks laterally and towards rear. Body greenish gray, with paler dorsal band broadening to slight diamonds on centre of segments; laterally black-brown with stripes as before, the most dorsal one limiting the dark area (except on segments with prolegs where it encroaches on the light area, leaving only a narrow band in rear of the small dorsal transverse tubercle on segment V).

Stage III.—Head pale ochreous, tinged with orange posteriorly and with slight black broken streaks laterally on cheeks. Body light olivaceous,

with dorsal pale band rather prominent and edged by dark wavy lines; three pale lateral bands, wavy and edged by black, these lines being more prominent than the bands themselves; black lateral oblique patch on fifth and sixth abdominal segments, narrowing dorsally behind small orange transverse tubercle; tubercles small, orange; slight black lunate mark on eighth abdominal segment.

Stage IV.—Head whitish, strongly orange posteriorly, this color extending to prothoracic segment; a black lateral line extending down to palpi and rather broken dorsally but distinctly joined behind the apices. Body whitish, sprinkled with dark dots which tend to form a broken subdorsal dark band; stripes lost in the ground color but the dark border lines, broken into spots, tend to give a general striped appearance; brown patch laterally above last two pairs of prolegs, crossed by darker band; prominent orange transverse wart; black lunate mark on eighth abdominal segment dorsally; tubercles orange; rear segment slightly orange.

Stage V.—Head pale flesh-color, mottled with purplish strigæ and tipped with orange posteriorly, with black lateral lines from base of palpi to rear of head; these lines not joining behind apices. Body pale gray, the anterior half of all abdominal segments washed with light brown (quite distinctive); a rather distinct subdorsal blackish band and a similar spiracular one; a dorsal black line dividing the pale diamond patches; tubercles and transverse wart orange; black lunate line behind eighth abdominal but no lateral patch; beneath pinkish with black patches; sides well filamented.

FOOD-PLANT.—Willow.

A description of the larval stages has already been given by R. R. Rowley (Ent. News, XXIV, 1913, p. 197) but, as his description is not very detailed and as it is possible, as he himself states, that he had the larvæ of two species mixed (the other being possibly *verecunda*), we have thought it advisable to supplement his notes by the above description drawn up from material received from Minneapolis, Minn.

Catocala irene Behr

OVUM.—Similar to those of *C. californica* and *C. faustina*.

LARVA.—*Stage I.*—Scarcely to be distinguished from those of *C. faustina* or *C. verecunda*. Head pale red-brown. Body greenish-gray, shading into purplish laterally and with three pale lateral lines of the ground color.

Stage II.—Head whitish, marbled with blackish stripes, with slight tinge of orange apically. Body pale gray-green, laterally greenish-black

with three pale waved stripes; a faint dorsal stripe with diamond shaped enlargements. Length, 11 mm.

Stage III.—Head pale with brown marbling, shaded with orange at apex and with black lateral border-lines, not meeting dorsally. Body light olive-brown with pale dorsal and lateral stripes as before, bordered with deep brown, the lower border of stripe II and the upper one of III especially prominent; transverse wart on fifth abdominal segment reddish with ochreous apex and shaded laterally with black; a black-brown lateral shade below this wart, broken by the pale stripes, deepest in color above stripe III and tending to extend along its dorsal margin towards anal segment; dorsal tubercles orange, larger and conical on eighth abdominal segment with slight black lunate marks behind them not meeting dorsally. Length, 17 mm.

Stage IV.—Head pale whitish, slightly orange apically below which is some brownish marbling; a black border line. Body very pale ochreous, with darker subdorsal stripe bordering the centrodorsal pale diamond patches and composed of numerous dots; a similar dark spiracular band, very heavy across the rear of the fifth abdominal segment. Pale stripes I and II of previous stage almost confluent, owing to lack of definite border lines and similarity to the ground color. Tubercles and transverse wart on fifth abdominal segment small, orange; a mere suggestion of a dark lateral shade on rear portion of fifth abdominal segment.

Stage V.—Head as before. Body pale ochreous caused by heavy brown sprinkling on a very pale ground; a prominent black-brown subdorsal stripe and a similar spiracular one; the dorsal diamond patches very distinct on account of the dark bordering band; a small orange wart dorsally on the fifth abdominal segment not broader than the diamond patches; dorsal tubercles orange with base black; those of the eighth abdominal segment conical but not prominent. Legs and prolegs pale flesh-color. The whole larva presents a rather flattened appearance. Length, 50 to 60 mm.

FOOD-PLANT.—Willow and poplar.

This larval description was drawn up from material of the var. *valeria* Hy. Edwards, received from Provo, Utah; in 1913, we only succeeded in rearing the larva to the third stage on willow; in 1914, using poplar as a food-plant, we brought several larvæ to maturity but all died before pupating.

Catocala faustina Strecker

The life-history published by us in *Psyche*, XX, p. 199, should be referred to *C. verecunda* Hulst; further breeding experiments conducted by us, in which the ova of known females were kept separate, brings us to the conclusion that *faustina* and *verecunda* are good species; ova of this latter species

hatch from one to two weeks earlier than do those of *faustina*; the young larvæ emerge from the whole batch of eggs at practically the same time, whilst *faustina* larvæ emerge singly, or in small numbers, over a very extended period of time, and it can happen that from a single batch of eggs one may have at the same time full grown larvæ and those just emerging. *Verecunda* may be bred fairly successfully in this section of the country on male willow catkins, but we have found great difficulty with *faustina* and, although we have succeeded in bringing a few larvæ to maturity, they have always died before pupation took place.

The ovum and first three larval stages are similar to those of *verecunda*; the last two stages show points of distinction as follows.

LARVA.—*Stage IV*.—Head whitish, lined and marbled with purple-brown, with rather prominent apical protuberances of a distinct orange color and narrow black lateral lines extending down to ocular region. Body slender, pale ochreous brown, marbled and dotted with small blackish dots and streaks; tubercles orange; hump of fifth abdominal segment large, orange, spotted with black; the pale dorsal band, enlarging somewhat into diamond marks, is defined laterally by rather darker colored subdorsal bands composed of fine black-brown speckles and bordered on each side by dotted dark lines; below this is a broad lateral irregular band bordered ventrally by a narrower darker spiracular band, below which the ground color is again paler; the lateral brown patch below the dorsal wart is only faintly visible, most noticeable on spiracular band; dorsal tubercles on eighth abdominal segment with orange color rather extended laterally, tending to form the usual lunate mark; filaments well developed. Length, 37 mm.

Stage V.—Head broad, front somewhat concave with two rather prominent apical bulges; general color whitish, heavily striated with dull purplish frontally above clypeus, with the apical bulges salmon-pink; a fine black lateral line to cheeks slightly broken behind the apices. Body rather flat and slender; color much as in preceding stage, being light olivaceous-brown with a rather definite pale dorsal stripe bordered by darker subdorsal stripes which, behind tubercle II on each segment, tend to deepen in color; dorsal wart of fifth abdominal segment prominent, ochreous, lined with black; the lateral brown shade is only visible in the stigmatal area where it shows as a lunate brown stripe; dorsal warts and a lunate mark behind tubercle II of eighth abdominal segment, deep orange; stigmata ringed with black. Prolegs, anal plate, and claspers, shaded with pinkish. Length, 57 mm.

FOOD-PLANT.—Willow.

Catocala briseis Grote

OVUM.—Hemispherical; the micropyle, situated at apex of egg, consists of several concentric rows of minute cells surrounded by a very slight rim, beyond which is an irregular encircling row of somewhat larger, irregularly hexagonal cells; the usual vertical ribbing is present, consisting of about 15 to 18 ribs arising from the micropylar area and branching irregularly to form 38 to 40 ribs at base of egg; fine transverse ribbing; color brown, mottled with yellowish. Diameter, 1.1 mm.

LARVA.—*Stage I (just emerged)*.—Head flat; pale red-brown. Body dirty green-gray, with three indistinct, rather broad, red-brown lateral stripes and traces of a fourth subventral line; general appearance without a lens is black-brown. Length, 3 mm.

After feeding, the lateral area becomes red-brown with three pale lateral stripes. Can at once be distinguished from the first stage of *unijuga* by its reddish head.

Stage II.—Head whitish ochre, marbled with black. Body blackish, with broad dorsal whitish area shading into ochreous laterally below tubercle II; this stripe is even in width and rather narrow on the thoracic segments, then broadening on the first four abdominal segments and extending to the region of tubercle V, narrowing again almost to a line behind a small black transverse dorsal wart on the fifth abdominal segment; on the first four abdominal segments an ochreous line crosses the pale area on the level of tubercle II; faint traces of pale lines crossing the dark lateral area. In later stages, the colors merge and are not nearly so contrasting.

Stage III.—Head pale purplish gray, tipped with orange and with a black lateral line bordering lobes. Body light brown, marbled strongly by longitudinal lines; on the first three abdominal segments two of these lines form indistinct subdorsal W marks behind tubercle II; laterally the segments are slightly tinged with black as far as the fifth abdominal segment; this segment has a small black or orange transverse dorsal wart, lateral and posterior to which the remaining segments are almost entirely velvety black, with the exception of a narrow dorsal pale stripe.

Stage IV.—Head pale, marbled with purplish, tipped with orange, bordered laterally not very heavily with black; the bands scarcely meeting behind apex of head. Body light brown, with numerous waved and dotted black lines which tend to form W marks dorsally behind tubercle II; dorsal pale diamond patches fairly distinct, due to bordering dark areas; wart on fifth abdominal segment orange brown, with a deep brown lateral patch extending to prolegs and crossed by three black bands. Tubercles, orange;

tubercle II on eighth abdominal segment raised, conical and followed by slight black oblique streak.

Stage V.—Head pale flesh-color, shading into orange apically, below which is purplish marbling; a rather narrow black border line. Body rather slender; purplish-brown, heavily dotted with black; dorsal tubercles distinct, orange; lateral tubercles small, pale; distinct dorsal diamond patches defined by dark dotted lines; two pale lateral stripes and a third subspiracular one are fairly distinct, especially on the rear portion of the fifth abdominal segment where they cross a diffuse light-brown patch and are accentuated on their margins by black shading; transverse wart on fifth abdominal segment purplish, lined with black, with the lateral patch of preceding stage paler and less defined, being light brown; fringes whitish-pink; beneath pale purple-pink, with deep black spots. Legs and prolegs pinkish. Length, 60 mm.

We were very successful in breeding large numbers of this species from ova received from various points in Northern Ontario and Manitoba; both poplar and willow were used as food-plants with equally good results.

Catocala grotiana Bailey

OVUM.—Very similar to that of *C. briseis* but larger.

LARVA.—*Stage I.*—Head reddish-black, marked laterally with gray but not strikingly so. Body dirty gray, reddish laterally, crossed by three wavy pale lines of ground color. Legs and prothoracic shield black.

Stage II.—Head pale ochreous, tinged with red and lined with black. Body laterally blackish, crossed by three pale waved lines; dorsally on the first eight segments, pale ochre broadening somewhat on the first abdominal segment and forming more or less of a diamond-shaped patch pitted by the dark tubercles and having a general checkered effect; a small dark transverse tubercle on fifth abdominal segment, posterior to which the remaining segments are almost uniform black with the exception of a narrow pale dorsal line.

Stage III.—Head pale, tipped with orange and with lateral black borderlines. Body whitish-yellow, lined with rows of black dots, especially evident preceding tubercle III, and just dorsad of same; broken black subdorsal patches may be present or absent; a black transverse dorsal wart on fifth abdominal segment with a heavy black lateral patch descending to prolegs; black dorsal crescents on rear of eighth and ninth abdominal segments.

Stage IV.—Head whitish, strongly tipped with orange below which is a black streak parallel to side of clypeus; lobes with purplish marbling and

black border lines. Body whitish, with irregular black dotting and streaks partially outlining the dorsal diamond patches; several dots and streaks above the spiracle; tubercles pale orange; dorsal wart on fifth abdominal segment tipped with orange, with a strong black lateral patch crossed above prolegs by broad whitish-pink curved stripe; black dots behind tubercle II on seventh abdominal segment and black crescent behind those of the eighth segment; fringes white. The amount of black present in this stage is quite variable.

Stage V.—Head flesh-colored, tipped with orange and heavily mottled below this color with purple which forms a perpendicular line descending from apex of lobe to above palpus and an inner line parallel to edge of clypeus and curving at apex to join the former line; black border to lobes broken behind the apices. Body pale whitish ochre, sprinkled with brown dots mixed with black; the black color defines the dorsal diamond patches on the rear portion of the first four abdominal segments and forms a few dots and streaks above the spiracle, especially on prothorax; wart on fifth abdominal segment arising from a heavy black base; lateral black shade much broken and crossed by a pale stripe above and below the spiracle; an oblique black stripe on eighth abdominal segment between tubercles II and III; fringes whitish. Legs faintly pink; prolegs whitish, striped with black on posterior side.

FOOD-PLANTS.—Willow and poplar.

The larva, which shows considerable affinity to *briseis* in the early stages, is vastly different when mature, approaching much closer to *pura* and *relicta* in appearance and amply establishing the validity of the species. The ova, from which we successfully reared several adults, were received from Provo, Utah.

Catocala unijuga Walker

OVUM.—Scarcely distinguishable from that of *briseis*; very slightly larger.

LARVA.—*Stage I.*—Head black. Body deep greenish black, with pale gray dorsal area and three faint stripes laterally. The black head at once separates it from *briseis* and allied species.

Stage II.—Head pale, heavily mottled with black. Body jet-black, except dorsally where there is a broad pale ochre band with a tendency to form diamond patches as far as the fifth abdominal segment, posterior to which it narrows to almost a line; on the first abdominal segment this band expands laterally towards the spiracular area; faint traces of three pale lateral lines.

Stage III.—Head flesh-color, heavily encircled with black and with frontal black M. Body laterally largely blackish, crossed by indistinct pale ochreous bands giving a mottled appearance; a prominent pale ochreous dorsal stripe, enlarging into diamond patches and spreading laterally over the whole first abdominal segment and partially over the second segment; slight black transverse dorsal wart on fifth abdominal segment, with lateral black shade extending to prolegs.

Considerable variation exists in the different broods in the amount of black coloring. Some have the lateral area much marbled with pale ochreous so that the general color appears to be pale ochreous with the borders of the diamond patches composed of strong geminate black lines broken on the fore part of each segment; in such cases, the black lateral patch on the fifth abdominal segment stands out much more clearly.

Stage IV.—Head small for the size of the body, heavily lined with black in front and with broad black lateral border; apices tipped with orange. Body mixed black and gray, due to a heavy black sprinkling on a pale ground which is almost covered; dorsal diamond patches fairly distinct, outlined by punctiform black lines; the anterior portion of first abdominal segment usually paler, as is also the fifth abdominal segment at times; small transverse wart dorsally on fifth abdominal segment, tipped with orange with a deep black lateral patch extending to between the prolegs; a black crescent dorsally on posterior portion of eighth abdominal segment; tubercles small, pale orange.

Stage V.—Head flesh-color, shading into orange apically with very heavy black lateral border; frontal black markings consist of a streak through center of clypeus, two streaks parallel to the upper part of clypeus, and a streak from the apex of each lobe to the mouth. Body light ochreous so heavily mottled with black that the general appearance is blackish with pale mottlings; dorsal tubercles pale ochreous, rather distinct; the most distinct features of the maculation are the pale dorsal diamond patches bordered with blackish and a pale stripe above the spiracle; laterally the first abdominal segment is often paler than the remainder of the body and the fifth abdominal is more heavily shaded with black, this being the remains of the patch of previous stages; transverse wart small, pale, marked with black laterally at base; tubercles II on the eighth abdominal segment rather larger than on other segments and with the usual black oblique streak behind; beneath pinkish with black spots; fringes pale.

FOOD-PLANTS.—Willow and poplar.

Rowley (Ent. News, XIX, 1908, p. 115) records five molts, but this is evidently an error; the normal number in this group is four.

We bred good series of adults from batches of ova received from various localities in Ontario and Manitoba.

Catocala semirelicta Grote

OVUM.— Similar to those of *C. briseis* and *C. unijuga*.

LARVA.— *Stage I*.— Head red. Body dirty green, with three pale lateral stripes; dorsal area slightly paler.

Stage II.— Head pale, faintly marbled with darker lines and encircled by a narrow black line. Body pale ochreous; laterally black with three pale lines; the dorsal ochreous area extends laterally to the spiracular area on the first abdominal segment and also on the posterior portion of the fifth and the anterior portion of the sixth abdominal segment, which distinguishes the stage at once from similar ones of either *unijuga* or *briseis*; tendency to diamond patches on the mid-abdominal segments dorsally.

Stage III.— Head pale, marbled with darker lines, tipped with orange, and bordered narrowly with black. Body pale ochre, marbled with deeper ochre in the shape of longitudinal lines and marked laterally with black which forms a species of zigzag black lateral line, broken on the first abdominal segment; a small dorsal transverse wart on fifth abdominal segment with a black lateral patch; tubercles orange.

Stage IV.— Head flesh-colored, rather broadly suffused with orange apically, marbled with purplish, and with a faint and broken black border. Body whitish, evenly striate longitudinally with black, closely approached, dotted lines, slightly tinged with ochre-brown laterally above the fringe; transverse wart of fifth abdominal segment tipped with ochreous, with indistinct black broken lateral shading extending to between prolegs; a black crescent behind tubercle II on the eighth abdominal segment; fringes whitish.

Stage V.— Head pale flesh-color, tinged with orange at apex rather broadly, marbled frontally with purplish with narrow black lateral border, more or less broken towards apex of lobes. Body whitish, evenly and heavily lined and marbled with black dots which at times form a prominent subdorsal stripe outlining the pale dorsal diamond patches; in other cases this subdorsal dark stripe is scarcely recognizable; transverse wart on the fifth abdominal segment ochreous, arising from a black base; the lateral black shade is reduced to some broken black streaks and dots, merely a slight accentuation of the general dark mottling; at times a dark spiracular stripe is fairly evident but this is often absent. Dorsal tubercles orange; lateral fringes white; spiracles pale ochreous, ringed with black; beneath whitish, with black patches. Legs pale orange; prolegs whitish.

FOOD-PLANT.— Poplar.

The mature larva is closely allied to that of *pura* and quite distinct from

those of *briseis* or *unijuga*. The ova from which we reared this species were received from Hymers, Ontario; the resulting imagines were strongly shaded with white before and beyond the reniform and with a prominent submedian black streak.

Catocala nevadensis Beutenmüller

OVUM.—Similar to that of *C. pura*.

LARVA.—*Stage I*.—Head dull red-brown. Body greenish gray, with paler dorsal area and three waved lateral lines.

Stage II.—Head whitish, with slight pink tinge and marbled slightly with black. Body pale creamy dorsally, with tendency to form the usual diamond patches; laterally olive-brown, crossed by three pale lines; below lines I and II are small lateral black patches on the rear of segments as far as fifth abdominal segment, which has a black lateral patch extending from a small transverse dorsal wart as far as line III; posterior to this segment the interspaceal area between the pale lines is rather heavily black. The olive-brown lateral area with its black dots renders the larva quite distinct from allied forms.

Stage III.—Head flesh-color, tipped with orange and faintly bordered by a broken black line much as in *semirelicta*. Body light olive-brown, with pale ochreous dorsal diamond patches and three lateral lines more or less bordered with black-brown, especially the diamond patches on rear of first four abdominal segments; there is a tendency on the posterior portions of the first two abdominal segments for the pale dorsal area to spread laterally, coalescing with the first pale stripe; transverse wart on fifth abdominal segment, orange, small, with heavy black lateral patch extending to prolegs; a black crescent posterior to tubercle II on eighth abdominal segment; tubercles, small, orange.

Stage IV.—Paler than in preceding stage. Head whitish, tinged with orange apically below which are brown marblings; laterally a narrow black-brown border composed of two parallel lines reaching from apex of lobes to region of the ocelli. Body whitish, with orange tubercles and an orange-brown transverse wart on the fifth abdominal segment; the lateral oblique black shade is broken up into some black markings in the region of tubercles II and IV; pale stripes faintly visible with border lines broken up into dots; a dark oblique line behind tubercle II on the eighth abdominal segment.

Stage V.—Very close to *pura*. Head pale flesh-color shading into orange apically, with purplish markings below apex and a narrow black lateral border line. Body pale greenish white, heavily pitted with brown

in more or less longitudinal rows; dorsal diamond patches relieved by dark shade lines; wart on fifth abdominal segment rather large, bounded laterally by tubercle II which is orange; the wart itself is dull orange with black marbling; no lateral shade; fringes whitish; spiracles pale, with black rim; beneath greenish white, with black patches. Legs pale ochreous.

FOOD-PLANTS.—Poplar and willow.

Catocala concumbens Walker

OVUM.—Rather more than hemispherical; very similar to that of *cara*; micropylar area, however, neither raised nor depressed, consisting simply of a number of small hexagonal cells situated at apical area of egg; from this area 18 to 20 radial ribs descend to the base of the egg; in the equatorial region secondary ribs arise independently in the interspaces between these main ribs, and these secondary ribs branch shortly once or twice before reaching basal area, so that the lower portion of the lateral area is lined with 60 to 70 ribs; fine transverse cross ribbing is present; color brown. Diameter, 1 mm.

LARVA.—*Stage I*.—Head pale red-brown. Body green-gray, with three brown lateral stripes and a similar subventral one.

Stage II.—Head white, heavily marbled with black-brown. Body deep purple-gray with geminate dorsal pale line and three lateral pale lines; beneath whitish.

Stage III.—Head white, apices of lobes orange with black longitudinal streaks, sides of cheeks with more or less black network. Body dorsally light brown, with pale geminate whitish dorsal stripes bordered by a brown line and coalescing towards the rear of each segment enclosing the usual diamond patches; laterally deep purplish with three pale stripes, the upper being well marked and forming the border line between the light dorsal and the dark lateral regions; on fifth abdominal segment dorsally a well-defined black transverse wart. Legs ochreous; prolegs blackish.

Stage IV.—Head whitish, streaked and marbled heavily with blackish purple; apex of lobes orange; a rather broad black lateral border to lobes. Body purplish-brown; the geminate dorsal stripe and three lateral stripes of the preceding stage may still be traced by their paler color and border of dark dotted lines; tubercles orange; dorsal wart of fifth abdominal segments prominent, reddish-brown; a pale brown oblique shade laterally on posterior portion of fifth and anterior portion of sixth abdominal segments crossed by the pale lateral stripes; tubercles II of eighth abdominal segment

with short oblique black stripes proceeding from them forward and downward; lateral filaments, short, whitish; beneath, whitish. Length, 30 mm.

Stage V.—Head pale pinkish, streaked heavily with deep purplish, tipped with orange and with broad black lateral band. Body deep purple brown, sprinkled with blackish dots; slight pale transverse wart on fifth abdominal segment and light brown lateral shade as before crossed by darker subdorsal and subspiracular bands; tubercles orange; lateral fringes short, pinkish; eighth abdominal segment dorsally with black crescent behind tubercles II; beneath pinkish. Legs light brown. Length, 60 mm.

FOOD-PLANTS.—Different kinds of low willows.

The final larval stage has been already noted by several authors (Saunders. Proc. Ent. Soc. Phil., II, 1863, p. 29) and Rowley has briefly recorded all the stages (Ent. News, XXI, 1910, pp. 112, 113).

***Catocala illecta* Walker**

OVUM.—Base flat; apex considerably flattened; otherwise hemispherical; micropylar area rather more extended than usual, consisting of small cells; from this area about 30 rather broad but scarcely raised radial ribs, a few of which are branched, descend to the base; these ribs are not prominent and under the lens have a granular appearance.

The ova are apparently laid in groups in crevices of the bark and then overlaid with a sort of thin albuminous cement as in *ultronia* and allied species, thus rendering observation difficult as the cement is not soluble in water. Our description was drawn up from a few unfertile ova, laid in a crevice of a paper bag, received from Prof. R. R. Rowley of Louisiana, Missouri.

The number of larval stages is not yet known but is presumably five, with the normal number of four molts.

***Catocala abbreviatella* Grote**

OVUM.—Hemispherical; the micropylar area rather extended and consisting of small, irregularly hexagonal cells; remainder of egg with strong vertical, unbranched ribs, about 18 to 22 in number, which nearly all attain the micropylar area, there being only an occasional rib inserted interspaceally in the equatorial zone; faint transverse ribbing; base flat; color gray. Diameter, 1 mm.

Received through the kindness of Mr. C. E. Dodge, who was successful in obtaining a few eggs from a Nebraskan female in the summer of 1914; the larvæ, unfortunately, did not hatch.

Catocala coccinata Grote

OVUM.—Rather large; hemispherical; base flat; micropyle situated in a circular group of minute cells at apex of egg, surrounded by a slightly raised rim, beyond which are a couple of irregular rows of somewhat larger cells; surface of egg prominently ribbed with about 19 rather coarse vertical ribs, nearly all of which attain the micropylar area; transverse ribbing very faint; color brown. Diameter, 1.2 mm.

LARVA.—*Stage I*.—Head black. Body pale gray, with prominent black tubercles with long setæ; on first four abdominal segments are lateral brown patches, and there are six longitudinal brown lines.

Stage II.—Head pale, lined with black. Body purplish gray with three pale ochreous lateral stripes, to which the six dark lines of the preceding stage act as border lines; tubercles black.

Stage III.—Paler than the preceding stage. Head heavily marked with black. Body pale purplish, with longitudinal dark lines enclosing alternate light and dark spaces and forming a geminate pale dorsal stripe enlarging into the characteristic diamond patches and three pale lateral stripes; dorsally on the fifth abdominal segment is a strong black hump.

Stage IV.—Head pale in the lower portion; apical area creamy orange, this color descending half way down along the sides of the lobes and enclosing a dark, blackish, mottled patch; a black lateral line bordering lobes. Body purple-gray, with the stripes of the preceding stage less distinct; on the first abdominal segment above tubercle III a slightly paler patch; on fifth abdominal segment dorsally a very strong fleshy horn-like wart; prominent dorsal warts on the eighth abdominal segment bearing an enlarged tubercle II and bordered posteriorly with black; faint ochreous shade laterally on fifth and sixth abdominal segments crossed by indistinct darker lines; tubercles orange; lateral fringe present.

Stage V.—Head grayish in lower portion with black spot on each side of the clypeus; apically whitish with faint orange tinge below which is a dull purplish tint slightly marbled with whitish; a faint black lateral border line. Body purplish-gray heavily speckled with darker dots; all stripes of preceding stages indistinct, the pale dorsal diamonds slightly relieved by darker subdorsal bordering stripe; the upper dark border line of the first lateral stripe and a broken wavy line on a level with tubercle III rather distinct; all tubercles orange; a rather indistinct pale patch on the first abdominal segment laterally, shaded with darker posterior to tubercle III; prominent conical smoky-brown horn on the 5th abdominal segment bordered anteriorly at base with whitish; posterior to this horn the pale dorsal

stripe is quite evident bordered by a darker line; a pale brown lateral shade over fifth and sixth abdominal segments crossed by two dusky stripes, the upper (spiracular) being very distinct; on eighth abdominal segment tubercle II is very prominent, conical, with the usual oblique brown dash behind it; fringes white; beneath greenish white tinged with pink.

FOOD-PLANT.—Oak.

Catocala ultronia Hübner

OVUM.—Laid in single rows in a crevice of bark (or fold of paper bag in confinement) and covered with a species of albuminous waterproof cement; circular, flattened greatly at both base and apex and resembling a miniature Dutch cheese; the sides show faint vertical ribbing, the ribs being broad, unbranched and of a rather granular character; color light brown. Diameter, 1 mm. The egg shows great similarity to that of *illecta*.

LARVA.—*Stage I*.—Head flat, pale red-brown, whitish frontally. Body of a general dirty black rather rough (after eating, smoother) appearance with small jet black tubercles which have long setæ. Under a lens the ground color is dirty gray-brown with three indistinct lateral red-brown stripes and a fourth broken subventral one; beneath dull olive.

Stage II.—Head dull red-brown streaked with black and whitish. Body deep greenish-gray with faint pale dorsal diamond patches and two waved lateral white lines.

Stage III.—Head pale ochre marked with black. Body deep black-brown lined with ochreous; dorsal tubercles reddish; fifth abdominal segment with a prominent dorsal hump and a lateral reddish patch preceded by pale shading; dorsally on first two abdominal segments pale streaks before tubercle II.

Stage IV.—Head bordered laterally with black, apex tipped with pinkish-red and marbled with purplish forming a slight blotch below the red color. Body pale to dark purplish with long pointed red-brown horn dorsally on the fifth abdominal segment shaded posteriorly with black; a ruddy lateral patch on same segment extending to between the prolegs and often preceded by pale shading; pale dorsal diamond patches and lateral stripes faintly visible; on first two abdominal segments there is often a white spot anterior to tubercle II; tubercles small, orange, arising from a whitish base; posterior to tubercle II on the eighth abdominal segment a black crescent; fringes pinkish.

Stage V.—Head pale purplish mottled with white frontally and shaded apically with pink; a heavy black border line. Body deep purplish heavily

mottled with black dots; on fifth abdominal segment a prominent dorsal red-brown pointed horn-like wart shaded with black around its base, and a rusty brown lateral patch crossed by a darker spiracular stripe and often preceded by whitish shading; dorsal tubercles pale orange, those of the first abdominal segment often preceded by a white dot, which is of rarer occurrence on the following segment; lateral tubercles small, whitish; lateral pale stripes scarcely to be traced; dorsal stripe rather evident behind the horn-like wart; an oblique black stripe posterior to tubercle II on the eighth abdominal segment and slight black sprinkling on the seventh one; fringes pinkish; beneath bright pink. Legs purplish marked with black.

FOOD-PLANTS.—Wild cherry, plum, and apple.

A description of the mature larva was given by Saunders in Can. Ent., VI, 1874, p. 147.

Catocala mira Grote

OVUM.—Practically similar to that of *ultronia*, circular, flattened strongly at both ends, with faint lateral ribbing; eggs laid in rows in a crevice and cemented over with a whitish waterproof mass.

LARVA.—*Stage I*.—Head pale red. Body dirty gray, with three broad lateral reddish lines and a fourth subventral one; tubercles black.

Stage II.—Head whitish, heavily marbled with black leaving a small space frontally. Body deep gray, paler dorsally, with three irregular whitish dorsal lines; tubercles black. When fully grown traces of pale dorsal diamond patches and a small red dorsal wart on the fifth abdominal segment are evident.

Stage III.—Head heavily marbled with black with traces of white dashes frontally; apex of each lobe strongly bulging so that viewed from the side the head appears concave frontally. Body dark gray on thoracic segments, paler dorsally on first four abdominal segments, posterior to fifth abdominal segment almost black with the exception of a narrow pale dorsal stripe; first four abdominal segments with geminate black subdorsal lines posterior to tubercle II; fifth abdominal segment with strong horn-like dorsal wart tipped with red and shaded with black at the base; a black lateral patch descending to between the prolegs; tubercles black.

Stage IV.—Head with two strong apical humps, deep black-brown with white shading frontally below the apex of the clypeus; a black streak on each lobe parallel to the side of clypeus and terminating in a small round dot-like patch; humps tipped with orange; lobes laterally heavily lined with black. Body pale gray, speckled with black with no very evident lines; slight blackish markings behind tubercle II on the first four abdominal segments;

dorsally on the fifth abdominal segment the pointed horn-like wart is reddish-brown and laterally there is a brown patch crossed by three blackish stripes; tubercles orange, II being fairly large and followed on the eighth abdominal segment by a short oblique black stripe; filaments whitish. Length, 25 mm.

Stage V.—Head whitish above the mouth parts, with black streak as in preceding stage; upper half deep brown with the apex tinged with red and strongly bulging; a double black border line laterally, filled with brown, beyond which the color is paler grayish, heavily mottled. Body whitish to greenish-gray sprinkled with dark dots and with orange-red tubercles; a prominent pointed red horn dorsally on the fifth abdominal segment, and an olive-brown shade laterally crossed by three darker stripes; posterior to tubercle II dorsally the dark dotted lines define diamond patches on each segment, otherwise no distinct stripes are visible; fringes white; beneath greenish-white with black spots.

FOOD-PLANT.—Thorn (*Crataegus*).

From a few ova received from Prof. Rowley of Louisiana, Missouri, under the name of *polygama* we were successful in rearing several imagines of what we believe to be *mira* Grote. According to the larva this species must be very close to *crataegi* Saunders, whose original description was largely drawn up from the larva; as, however, we were unable to make our larvæ entirely fit in with Saunders' description and as we have never had the opportunity of breeding the true *crataegi* we keep the species separate. The adults differ from *crataegi*, just as indicated by Grote, in the lack of contrasting shades on primaries and the deeper yellow of secondaries; Grote's figure (Ill. Essay Pl. IV, fig. 43) is however very misleading and like most of the figures in the work far too highly colored. Hampson (Cat. Lep. Phal., XII, p. 166) makes both *mira* and *blandula* forms of *crataegi*, but *blandula* is certainly distinct as our breeding results have shown, and *mira* in our opinion should also be considered a valid species until at least the larval history of *crataegi* is fully known.

Catocala blandula Hulst

OVUM.—Similar to those of *ultronia* and *mira*; circular, flat at both ends, cheese-shaped, laid in rows in a crevice and covered with a white, water-proof cement.

LARVA.—*Stage I*.—Head pale ochreous brown. Body pale olive-gray, with five red brown lateral lines, the first subdorsal on a level with tubercles I and II, the second above tubercle III, the third below III, and tending to broaden around lower edge of same partially enclosing the spiracle, the

fourth on a level with tubercle V, much broken and not continued beyond the fourth abdominal segment, the fifth below tubercle V and at the base of the prolegs; beneath are faint traces of central reddish-brown patches. Length (just emerged), 4 mm.

Stage II.—Head pale gray marbled with black-brown which forms two stripes running obliquely backward from vertex of clypeus to apex of head. Body now appears dirty black-brown with the pale whitish color of the previous stage showing distinctly as a dorsal stripe forming diamond-shaped enlargements as far as the fourth abdominal segment and posterior to this evenly broad; two whitish waved lateral lines in the area between tubercles II and III, the latter tubercle being just touched by the lower line; on the first four abdominal segments the dorsal diamond patches are only separated from the first pale lateral line by a thin black line and show traces of a centrodorsal dark line and a broken dark line anterior to tubercle II; below tubercle IV is a third pale lateral line; tubercles with the exception of I rather large, black, laterally usually ringed with white; spiracle ringed with white. When full-grown traces of a white dorsal wart on fifth abdominal segment are visible.

Stage III.—Head whitish marbled with black, stripes as before but connected apically with a black lateral band which curves around sides of head to the ocellar region. Body pale whitish marbled and marked with velvety black; dorsal pale line of previous stage much broadened on metathoracic and first two abdominal segments into Λ shaped patches with apex pointing forward and situated between tubercles II of each segment; these marks are greatly accentuated by broad velvety black shading extending forward from tubercle I of the following segment and broadest at the apex of the Λ which is filled with a cream-colored shade; on the third and fourth abdominal segments these marks are present but much reduced in size; posterior to the fifth abdominal segment the dorsal stripe is evenly broad and the whole lateral area more or less suffused with black, sharply defined anteriorly by a line anterior to tubercle II of the fifth abdominal segment which shows dorsally a small orange wart; tubercle II slightly tinted with orange, especially on rear segments; traces of three pale waved lateral lines; lateral area on anterior portion of fifth abdominal segment rather paler, only slightly mottled with olive-brown; slight traces of lateral filaments. Length, 18 mm.

Stage IV.—Head pale gray marbled with brown with black blotch near the apex of each lobe tipped above with orange; a black encircling band. Body green-gray, tubercles orange, II being rather large; a small orange dorsal hump on the fifth abdominal segment and a lateral orange patch extending to the anterior portion of sixth segment; there is a heavy sprink-

ling of black dots which form more or less broken longitudinal lines; the most prominent feature is the deepening of the dark, subdorsal lines bordering the dorsal diamond patches on the metathorax and first four abdominal segments and the lateral line just below tubercle II, these now forming W marks more or less filled in with black and enclosing tubercle II; a short oblique black line posterior to tubercle II on the eighth abdominal segment; lateral filaments pale; beneath white with black central patches. Length, 30 mm.

Stage V.— Head whitish marbled with pale purplish which forms a blotch below apex of head and above which is a slight pink shade; a black lateral bordering band, descending to palpi and tinted with orange in its upper half. Body green-gray to purple-gray, heavily mottled with olive-brown dots; dorsally the lines of dots bordering the dorsal diamond patches are fairly distinct on the rear portion of each segment; tubercles orange, II being quite prominent; the dorsal hump on the fifth abdominal segment is slightly larger than tubercle II, gray, lined with pinkish, rather truncate and pointed backward; tubercle II of the eighth abdominal segment conical, margined posteriorly with orange and black; yellow-orange patch laterally on fifth abdominal segment broken by pale dorsal stripe and crossed by deeper supra- and subspiracular bands; filaments whitish. Length, 42 mm.

FOOD-PLANT.— Thorn (*Crataegus*).

A few ova of this species were received from Hymers in Northern Ontario and successfully reared to the imaginal stage. The larva is quite distinct from that of *mira* and the species is undoubtedly a valid one.

***Catocala similis* Edwards**

OVUM.— Similar to that of *mira* and laid in a similar manner.

LARVA.— *Stage I*.— Head and tubercles black. Body pale gray with three brown lateral lines and a fourth subspiracular one.

Stage II.— Head black. Body light purple-brown with pale grayish dorsal stripe showing traces of diamond patches, two whitish lateral stripes, and traces of a pale subspiracular stripe.

Stage III.— Much as in preceding stage, head slightly lined with white; a geminate pale dorsal stripe broadening at intervals to form diamond patches; three pale waved lateral stripes with dorsal border lines; a slight black wart dorsally on the fifth abdominal segment; tubercles black.

Stage IV.— Head white, tipped with orange and heavily marbled with black, leaving a white stripe on each side of the clypeus. Body purple-brown with stripes of preceding stage much fainter and border lines broken

up into dots giving a general mottled appearance; on fifth abdominal segment a small black dorsal wart, tipped with orange, and a diffuse blackish lateral shade; tubercles, notably II, orange with black oblique dash posterior to II on the eighth abdominal segment.

Stage V.—Head white, slightly tipped with reddish below which is heavy purple-brown marbling; a narrow black lateral border-line to lobes. Body rather evenly dark brown, very heavily mottled; dorsally the diamond patches are visible on the rear portion of each segment and laterally faint traces of pale stripes may be discovered; on the fifth abdominal segment is a small transverse dorsal wart, blackish, tipped with white, posterior to which the rear portion of the fifth and the anterior portion of the sixth segments are rather darker than the general ground color; tubercles pale reddish with a whitish base, tubercles I and II on first abdominal segment being however often black with a slight whitish patch lateral to them. Legs pinkish. Length, 35 to 40 mm.

FOOD-PLANT.—Oak.

Catocala micronympha Guenée

OVUM.—Similar to those of *ultronia*, *mira* and *similis*, laid in a crevice and cemented over in the same manner.

LARVA.—*Stage I.*—Head brown-black. Body pale gray with traces of a brown stripe on a level with tubercle II; two lateral brown stripes, the second one touching a series of brown spots resting on tubercle III of which those on the first four abdominal segments are most prominent; traces of a subspiracular brown line; tubercles black.

The young larva is quite typical of the oak-feeders.

Stage II.—Head white frontally with an open black V above the apex of the clypeus and two dark dots; laterally striated with black. Body much as before when freshly over the molt but later approaching close to the following stage, owing to a darkening of the ground color.

Stage III.—Head white frontally with a black dot on each side of the clypeus and a black V mark above the apex of same; between the forks of this V and laterally on lobes are longitudinal black striations. Body pale yellowish, shaded on the segments posterior to the fifth abdominal with black; a white geminate dorsal line forming diamond patches as far as the fifth abdominal segment, these being defined outwardly with blackish posterior to tubercle II on each segment; three pale lateral stripes edged with brown and traces of lateral brown patches; a small white wart dorsally on the fifth abdominal segment and a not very pronounced blackish lateral shade; beneath white with strong black patches. Prolegs pale.

Stage IV.—Very similar to the preceding stage with dark subdorsal patches on the rear of the first four abdominal segments accentuated and black lateral patch stronger.

Stage V.—Head whitish tipped with orange-brown, below which is a black network of lines; a black bordering stripe to lobes composed of interlaced lines and filled with orange in its upper portion. Body whitish-gray dotted and streaked with black; pale dorsal diamonds rather distinct owing to the black bordering lines of dots; lateral to these on the posterior half of the first four abdominal segments are black shade dashes enclosing tubercle II; tubercles orange, ringed with black; hump of the fifth abdominal segment bluntly conical, whitish, with deep brown lateral patch crossed by three velvety black stripes and preceded by some palish shading extending to tubercle II of fourth abdominal segment; a similar pale area laterally on the first abdominal segment; traces of pale lateral stripes due largely to the accentuating lines of dark dots; a black oblique stripe posterior to tubercle II on the eighth abdominal segment; lateral fringe sparse; beneath greenish white with deep brown patches. Length, 30 to 40 mm.

FOOD-PLANT.—Oak.

Ova received from Mr. Reiff of Boston labelled *jacquenetta* were the source of the above notes, but all the larvæ perished in the pupal stage so we were unable to verify the identification, although we presume it to be correct.

Article VI.—NOTES AND DESCRIPTIONS OF ITONIDIDÆ
IN THE COLLECTIONS OF THE AMERICAN MUSEUM
OF NATURAL HISTORY

By E. P. FELT, State Entomologist, Albany, N. Y.

The classification of the myriad and diversified gall midges has progressed to such an extent that it is desirable to study material characterized before the present system had been satisfactorily worked out.

Through the courtesy of Dr. F. E. Lutz, Associate Curator of Invertebrate Zoology, it was possible not only to examine but to make microscopic preparations of some of the species described by William Beutenmuller, provided no unique specimens were subjected to the hazards of mounting under glass. This has permitted referring a number of species to the more closely defined modern genera and the detection of a few synonyms not previously known. Advantage has also been taken of this opportunity to characterize more fully several species.

The following gives the results of these recent studies.

Lasioptera podagræ Beutenmuller is a synonym of *Neolasioptera erigerontis* Felt. This error was primarily due to misidentification of the food-plant.

Cecidomyia clavula Beutenmuller, described in Can. Ent., XLV, 1913, p. 416, is a species of *Lestodiplosis*. It is entirely different from the *Cecidomyia clavula* Beutenmuller described in the Bull. Amer. Mus. Nat. Hist., IV, 1892, p. 269, a species of *Lasioptera* characterized in the imago in Bull. Amer. Mus. Nat. Hist., XXIII, 1907, p. 396, and undoubtedly the true maker of the gall. *Lestodiplosis* is an inquiline.

Cecidomyia rudbeckiæ Beutenmuller, described in Bull. Amer. Mus. Nat. Hist., XXIII, 1907, p. 388, is also a species of *Lestodiplosis*, an inquiline and not the maker of the deformity with which it was associated.

A reference of *Cecidomyia verbenæ* Beutenmuller, described in Can Ent., XXXIX, 1907, p. 306, to *Itonida* was confirmed by the study of a microscopic preparation made from type material.

Cecidomyia vernoniæ Beutenmuller, described in the Bull. Amer. Mus. Nat. Hist., XXIII, 1907, p. 389, is one of the trifli and probably inquiline, though the condition of the material available does not permit a positive generic reference.

Cecidomyia nyssæcola Beutenmuller, described in the Bull. Amer. Mus. Nat. Hist., XXIII, 1907, pp. 387–388, is likewise a member of the trifli and,

like the preceding, the condition of the material does not permit a definite generic reference.

Cecidomyia unguicola Beutenmuller, described in Bull. Amer. Mus. Nat. Hist., XXIII, 1907, p. 388, cannot be referred to a definite genus owing to the condition of the scanty material available.

Studies of microscopic preparations of other specimens permitted definite generic references and in addition to the original description we have given below structural details impossible of discernment except in balsam preparations.

***Dasyneura meibomiæ* (Beutenmuller)**

Cecidomyia meibomiæ BEUTENMULLER, Bull. Amer. Mus. Nat. Hist., XXIII, 1907, p. 390; Can. Ent., XLV, 1913, pp. 415-416.

The larva and gall of this species were first described and later the adults. These were characterized as follows.

Male and female.—Eyes large, contiguous at the vertex, black; face semi-translucent, dull orange red. Antennæ yellowish brown with erect black hairs. Thorax dull, semi-translucent red, with rather long, blackish hairs in grooves on top, forming two parallel lines, and a few hairs at the sides; scutellum dull semi-translucent red. Abdomen dull, semi-translucent, orange red, sparsely with brown black hairs; tip of abdomen blunt. Under side of body dull red. Legs fuscous. Expanse, 3.50 mm. Length, 1.33 mm.

The following structural details were drafted from microscopic mounts made from the type material.

Male.—The antennæ about three-fourths the length of the body, sparsely haired; 16 segments, the fifth with a stem about three-fourths the length of the cylindrical basal enlargement, which latter has a length one-half greater than its diameter, a sparse subbasal whorl of moderately short setæ, and subapically an irregular band of long, strongly curved setæ. Terminal segment somewhat produced, narrowly oval, with a length nearly three times its diameter. Claws rather long, moderately stout, and with a moderately short tooth near the basal third. The pulvilli a little shorter than the claws. Genitalia: basal clasp segment moderately long, stout, terminal clasp segment rather short, somewhat swollen basally, curved. Dorsal plate rather long, deeply and narrowly emarginate, the broad lobes nearly parallel and narrowly rounded apically. Ventral plate rather broad, deeply and triangularly emarginate, the lobes tapering to an irregularly truncate, setose apex. Halteres rather short, stout, setose externally and irregularly tuberculate distally.

Female.—The antennæ about half as long as the body, sparsely haired; 15 to 17 sessile segments, the fifth with a length about one-half greater than its diameter, the terminal segment produced, with a length about three times its diameter and tapering to a narrowly rounded apex. Palpi: first segment short, quadrate, the second one-half longer, broad, the third twice the length of the first, slender, and

the fourth a little longer than the third. Ovipositor when extended about half the length of the abdomen, the terminal lobes rather broad, with a length three times the width, tapering distally and very sparsely setose.

New York State Museum number, *a*2861.

***Hyperdiplosis meibomiifoliæ* (Beutenmuller)**

Cecidomyia meibomiifoliæ BEUTENMULLER, Can. Ent. XXXIX, 1907, p. 306.

An examination of the single male in the type material showed that it was undoubtedly referable to the trifoli. The original description is as follows.

Male and female.—Eyes black. Thorax and abdomen pale orange, the latter somewhat darker dorsally. Antennæ and legs fuscous. Wings blackish, hyaline. Length, 1.25 to 1.50 mm.

The following technical details were drafted from a microscopic preparation.

Female.—Antennæ nearly as long as the body, sparsely haired; 14 segments, the fifth with a stem three-fourths the length of the cylindrical basal enlargement, which latter has a length one-half greater than its diameter, basally a sparse whorl of stout setæ and subapically a band of longer coarser setæ. Low circumfili occur near the basal third and apically. Terminal segment slightly produced and with a slender setose finger-like process about three-fourths the length of the enlargement. Palpi: first segment short, subquadrate, the second nearly three times its length, the third a little longer and more slender than the second and the fourth about as long as the third, the third vein joining the margin of the wing well beyond its apex. Claws long, slender, simple and strongly curved, almost forming a right angle. The pulvilli less than half the length of the claws. Ovipositor short, with a length about one-third that of the abdomen, the lobes narrowly oval, with a length three times the width and sparsely setose.

New York State Museum number, *a*2863.

***Itonida myricæ* (Beutenmuller)**

Cecidomyia myricæ BEUTENMULLER, Can. Ent. XXXIX, 1907, p. 306.

The original description is as follows.

Male and female.—Eyes dark brown; front semi-translucent, sordid white. Antennæ as long as the body, fuscous; first and second joints semi-translucent, white. Thorax dull brown, smooth, with two yellowish longitudinal lines on the dorsum; posterior portion and scutellum dull amber-yellow, sides of thorax dull amber-yellow marked with brown. Abdomen dull amber-yellow above and below, sparsely beset with brown hairs. Legs fuscous. Wings hyaline, with black scales. Halteres semi-translucent, yellowish. Length, .75 to 1 mm.

The following technical details were drafted from microscopic preparations made from the type material.

Male.—Antennæ with 14 segments, the fifth having stems with a length one and one-half times and twice their diameters, respectively; basal enlargement subglobose and with a circumfilum reaching nearly to the middle of the basal portion of the stem; distal swelling with a length nearly one-half greater than its diameter, a distinct constriction near the basal third and moderately low circumfili basally and subapically, the latter not reaching the tip of the segment; terminal segment somewhat produced, the basal portion of the stem with a length nearly four times its diameter, the distal enlargement subcylindrical, tapering slightly distally, with a length fully twice its diameter and apically with a rather short, stout finger-like setose appendage. Palpi: the first segment irregular, the second a little longer, broader, the third one-half longer and more slender than the second and the fourth one-half longer and more slender than the third. Eyes holoptic. Third vein uniting with the margin well beyond the apex of the wing. Claws long, simple, the pulvilli about half the length of the claws. Genitalia: basal clasp segment moderately long, stout; terminal clasp segment rather long, stout, evenly curved; dorsal plate, short, broad, deeply and roundly emarginate, the lobes tapering to a narrowly rounded apex; ventral plate a little longer, broad, broadly and roundly emarginate, the lobes rather broadly rounded; style moderately long, stout.

Female.—Antennæ with 14 segments, the fifth with a stem one-half the length of the cylindrical basal enlargement, which latter has a sparse basal whorl of stout setæ, a subapical band of rather long, slender setæ and moderately high circumfili at the basal third and apically. Terminal segment produced, the enlargement subcylindrical, with a length fully three times its diameter and apically a short, somewhat irregular setose, finger-like appendage. Ovipositor when extended about as long as the abdomen, the terminal lobes tapering, slender, the length about four times the greatest width and sparsely setose. Other structural characters practically as in the male.

New York State Museum number, a2862.

This species runs in our table near to *Itonida tecomiæ* Felt, from which it is very easily separated by a number of characters.

Article VII.—CONTRIBUTIONS TO THE SNAKE CREEK FAUNA

WITH NOTES UPON THE PLEISTOCENE OF WESTERN NEBRASKA

AMERICAN MUSEUM EXPEDITION OF 1916

BY W. D. MATTHEW

Plates IV-X

The line drawings of this article are by Lindsey M. Sterling; the photographs by Albert Thomson.

In 1908 the writer and Mr. Harold Cook investigated a locality for fossil bones of which Mr. Cook had heard from neighbors south of the James H. Cook ranch at Agate, Nebraska. It was found to be extraordinarily rich in fragmentary remains scattered along the southern edge of the plains that lie between the Niobrara and North Platte valleys. The fossils were exposed at the edge of the breaks leading down into a number of dry creeks — Snake, Sheep, Spotted Tail, and Dry Spotted Tail Creeks — and occurred in a thin irregular deposit of sand and gravel, mostly unconsolidated, resting on the eroded and pockety surface of a light buff-pink-colored, sandy clay beneath. Both formations were fossiliferous and were regarded as being local phases of the Ogalalla and Arickaree formations, respectively, of Darton. The names of Snake Creek and Sheep Creek beds were given to these local phases for convenience in faunal correlation.

From the older Sheep Creek beds were obtained a number of skeletons of *Merychippus* and skulls, jaws, etc., of camels, Carnivora, etc., all indicating an early phase of the *Merychippus* zone equivalent to or slightly older than the Mascall and Deep River of Montana, distinctly older than the Pawnee Creek beds of Colorado. The Snake Creek beds yielded a large fauna, mostly of fragmentary material which appeared to be of early Pliocene age. The exact nature of the Snake Creek deposits was not very clear; they were obviously river-channel deposits, but in some of the outcrops the fossils and coarse material appeared to be partly remanié, concentrated through removal of the sand by subsequent wind action.¹

The locality was visited subsequently by parties from the Carnegie and Amherst Museums and in 1914 Dr. Sinclair secured for the Princeton Museum a large collection of Snake Creek fossils and described a number of new forms.² Mr. Cook made a number of visits from time to time and

¹ Matthew and Cook. 1909. A Pliocene Fauna from Western Nebraska. Bull. Amer. Mus. Nat. Hist., XXVI, pp. 361-414.

² Sinclair, W. J. 1915. Additions to the Fauna of the Lower Pliocene Snake Creek Beds, etc. Proc. Amer. Phil. Soc., LIV, pp. 73-95.

has also obtained a large collection and described a few new types.¹ In the spring of 1916 he secured from one of the pockets a remarkably fine skeleton of *Pliohippus* which is now in the American Museum collection. During the summer of 1916 the American Museum party in charge of Mr. Albert Thomson worked for part of the season in the great fossil quarry at Agate, and Mr. A. C. Whitford was detailed from this party to resume investigations in the Snake Creek locality with Mr. George Stoll as assistant. As the result of about a month's work a considerable collection was secured which is described in the following contribution.

Since the earlier exploration in 1908 the work of Dr. Merriam in the later Tertiary faunas of the Pacific Coast has added largely to the data for exact correlation of the later Tertiary mammal faunas of the United States, and has afforded evidence strongly suggesting that the Snake Creek fauna might in fact be a composite and not all of the same age.² Some doubt on this point had been expressed by Matthew and Cook in the early description. Unfortunately, the records and observations of the subsequent collecting have not been exact enough to clear up this doubt; but there seems to be some reason to believe that different fossiliferous pockets may be of different ages, ranging from late Miocene to early Pliocene. The writer purposes to devote some time next season to this problem.

The fauna is at all events a remarkably full one. Thirty-nine genera of mammals are listed here and it is probable that the number will be considerably increased by future collecting. Nearly all the known genera of the Upper Miocene and Lower Pliocene are present. The material is mostly fragmentary, but a number of more complete specimens have been secured, and the great numbers of individuals afford a much surer basis for distinguishing species than is usually the case in vertebrate palæontology. It will be understood that the "species" as here listed usually include a rather wide range of variation. They correspond to the older concept of the term, and by no means to the fine splitting that is customary among modern systematic zoologists. Such hair-splitting does not seem desirable at present in vertebrate palæontology, even if it be practicable on our usually fragmentary material. After all the larger novelties have been recognized and put on record it will be time enough to classify the minor differences

¹ Cook, H. J. 1912. Faunal Lists of the Tertiary Formations of Sioux Co., Nebraska. Neb. Geol. Sur. Rep., VII, pp. 33-45. 1914. A New Canid from the Lower Pliocene of Nebraska. Idem, part 7, pp. 49-50, Pl. I-III. 1915. Note on the Dentition of *Amphicyon amnicola*. Idem, part 10, pp. 57-58, Pl. I. 1915. Notes on the Geology of Sioux Co., Neb., etc. Idem, part 11, pp. 59-75, Pl. I.

² Dr. Merriam has not at the date of writing published this opinion, so far as I am aware; but the evidence that he has brought forward in a series of articles in the California University Geological Bulletin points very strongly to that conclusion, as he has made clear in discussions before the Palæontological Society.

and consider their nature and causes. That is very nearly the status at which systematic mammalogy has arrived; but we are a long way from having reached it with most fossil mammal faunas.

Although I have not listed fossil anthropoids as part of the fauna, it may be well to repeat that certain isolated teeth in the collection, provisionally referred to *Prosthennops*, are singularly like those of anthropoid apes. See Matthew and Cook, 1909, p. 390.

SNAKE CREEK FAUNAL LIST

Revised, 1917

("P", in Princeton collection but not represented in American Museum; "H. C.," Harold Cook collection)

Carnivora (Feræ)

Canidæ

<i>Pliocyon medius</i> Matthew	skull; parts of jaw
" <i>amnicola</i> M. and C.	lower jaw
" sp. max.	parts of jaws
<i>Ælurodon haydeni validus</i> M. and C.	lower jaws, teeth
" <i>sævus secundus</i> M. and C.	" "
" <i>wheelerianus taxoides</i> Hatcher	" "
<i>Tephrocyon mortifer</i> Cook	" "
" <i>hippophagus</i> M. and C.	upper and lower jaws
" <i>temerarius</i> (Leidy)	lower jaws
" <i>confertus</i> , new species	"
<i>Leptocyon vafer</i> (Leidy)	"

Procyonidæ

<i>Probassariscus antiquus</i> (M. and C.)	part of jaw
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Mustelidæ

<i>Brachypsalis modicus</i> , new species	upper and lower jaws
" <i>obliquidens</i> Sinclair	lower jaw
<i>Martes glareæ</i> Sinclair	lower jaws

Ursidæ

<i>Indarctos</i> sp.	m ² (H.C.); skel. bones
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Felidæ

<i>Pseudælorus intrepidus sinclairi</i> , new var.	lower jaws
? <i>Felis</i> cf. <i>maxima</i>	teeth, bones
Felinæ and Machærodontinæ indet.	bones

Rodentia (= Glires)

<i>Mylagaulus</i> cf. <i>monodon</i>	teeth, lower jaws
<i>Dipoides tortus</i> Leidy	upper and lower jaws
“ <i>curtus</i> M. and C.	lower jaw
<i>Amblycastor fluminis</i> , new gen. and sp.	upper and lower jaws
<i>Geomys</i> cf. <i>bisulcatus</i> Marsh	lower jaw

Edentata (Xenarthra)

? <i>Megalonychid</i> gen. and sp. indet.	claw; navicular (P.)
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Proboscidea**Mastodontidæ**

<i>Zygodontodon</i> sp.	teeth
<i>Trilophodon</i> (= <i>Gomphotherium</i>) sp.	“

Perissodactyla**Rhinocerotidæ**

<i>Teleoceras</i> sp.	lower jaw, teeth, etc.
<i>Aphelops</i> ? <i>crassus</i> (Leidy)	upper and lower jaws, etc.
<i>Peraceras</i> ? <i>superciliosus</i> Cope	skull, etc.

Equidæ

? <i>Archæohippus</i> sp.	teeth (P.)
<i>Parahippus cognatus</i> Leidy	upper and lower jaws
<i>Hypohippus</i> ? <i>affinis</i> Leidy	teeth
“ <i>pertinax</i> , new species	upper and lower jaws
<i>Merychippus insignis</i> Leidy	“ “ common
“ <i>calamarius</i> (Cope)	“ “ “
<i>Protohippus perditus</i> Leidy	teeth
“ <i>placidus</i> Leidy	upper and lower jaws
<i>Pliohippus mirabilis</i> (Leidy)	teeth
“ <i>leidyanus</i> Osborn	skeleton, etc.
<i>Hipparion occidentale</i> Leidy	teeth
“ <i>gratum</i> Leidy	“

Artiodactyla**Dicotylidæ (= Tagassuidæ)**

<i>Prosthennops</i> cf. <i>crassigenis</i> Gidley	jaws
“ cf. <i>serus</i> Cope	teeth

Oreodontidæ

<i>Metoreodon relictus</i> M. and C.	upper and lower jaws
“ <i>profectus</i> M. and C.	“ “
<i>Pronomotherium siouense</i> Sinclair	lower jaw (P)

Camelidæ

<i>Pliauchenia gigas</i> M. and C.	skull, teeth, bones
“ cf. <i>vera</i> Matthew	jaws, teeth
“ sp. max. indesc.	upper jaw
<i>Alticamelus procerus</i> M. and C.	skull, jaws, skel. parts, etc.
“ sp.	upper jaw, teeth
<i>Procamelus</i> cf. <i>occidentalis</i> Leidy	jaws, teeth
“ cf. <i>robustus</i> Leidy	“ “
“ cf. <i>gracilis</i> Leidy	“ “
<i>Protolabis princetonianus</i> Sinclair	skull (P), jaws, etc.
? “ sp.	jaws, teeth

Palæomerycidæ

<i>Dromomeryx whitfordi</i> Sinclair	jaws
“ sp.	jaw fragments, teeth
<i>Drepanomeryx falciformis</i> Sinclair	horn (P)

Cervidæ

<i>Blastomeryx elegans</i> M. and C.	jaws
“ <i>wellsi</i> Matthew	“
<i>Cervavus sinclairi</i> , new species	“
“ sp.	jaw fragments, teeth

Antilocapridæ

<i>Merycodus necatus</i> Leidy	skulls, jaws, etc.
“ sp.	teeth

?Bovidæ (or Giraffidæ)

<i>Neotragocerus improvisus</i> M. and C.	horn
<i>Cranioceras unicornis</i> , new species	“ , ? jaw

Aves

<i>Aquila danana</i> ? Marsh	metatarsus (P)
<i>Geranoaetus</i> sp.	“
<i>Buteo</i> near <i>borealis</i>	(P)

Reptilia

<i>Alligator</i> sp.	jaw, limb bones, etc.
<i>Testudo</i> sp. max.	fragments of shell
Lacertilians indet.	jaws

Amphibia

Plicagnathus matthewi Cook part of jaw (H. C.)

Pisces

Ameiurus sp. jaw, parts skull, etc.

CARNIVORA

Canidæ

Tephrocyon Merriam

The practical distinction of this genus from *Canis* in the lower jaws, which are most frequently found, is the invariable presence of a well developed paraconid on m_2 . This is not uncommon as a vestigial cusp in some modern species of *Canis*, especially the Central and South American species and the jackals of the Old World. I have not observed it in the foxes. The genus includes the structural ancestors of *Ælurodon*, *Canis*, *Vulpes*, *Lagopus*, not of *Cyon*, *Icticyon*, *Lycaon* or of any Tertiary genera other than *Ælurodon*. Four species are recognized in the Snake Creek as follows:

Tephrocyon mortifer Cook. Size of wolf. Jaws heavy, long, premolars large.

Tephrocyon hippophagus Matthew & Cook. Size of coyote; but jaw decidedly shorter, teeth stouter, less compressed.

Tephrocyon temerarius Leidy. Size of fox; but jaw decidedly shorter, teeth stout, not compressed, premolars larger, metaconid of m_1 large, m_2 more than half length of m_1 , heel of m_1 wider, about one-third length of tooth.

Tephrocyon confertus sp. nov. Somewhat smaller than *T. temerarius*. Carnassial more compressed, premolars decidedly smaller, m_2 less than half m_1 , metaconid of m_1 small, heel of m_1 about one-fourth length of tooth. Canine quite small.

There are two other described species of *Tephrocyon*, the type *T. rurestris* (Condon), which is from the Mascall, and *T. kelloggi* Merriam from the Virgin Valley formation. Their characters and relations to the Nebraskan species have recently been summarized by Dr. Merriam.¹ Other undescribed species from various horizons are apparently represented in the American Museum's collections, the genus covering a fairly wide range of variation.

¹ Merriam. 1913. Notes on the Canid genus *Tephrocyon*. Univ. Cal. Publ., Bull. Dept. Geol., VII, pp. 359-372. Separata, Sept. 23, 1913.

It appears to constitute the ancestral group from which *Canis*, *Vulpes*, *Lagopus*, *Urocyon*, all in fact of the typical group of modern Canidæ, are derived. In turn, it is derived from *Cynodesmus* of the Lower Miocene, in which the carnassial shear is more transverse, the brain-case smaller, brain more primitive, and feet shorter, less compressed, more nearly pentadactyl. The European *Galecynus* may be identical with *Cynodesmus*, although from a somewhat later horizon, but its teeth are not sufficiently known for exact comparison. The generic reference of the Oligocene American species of typical Canidæ requires revision; two generic names

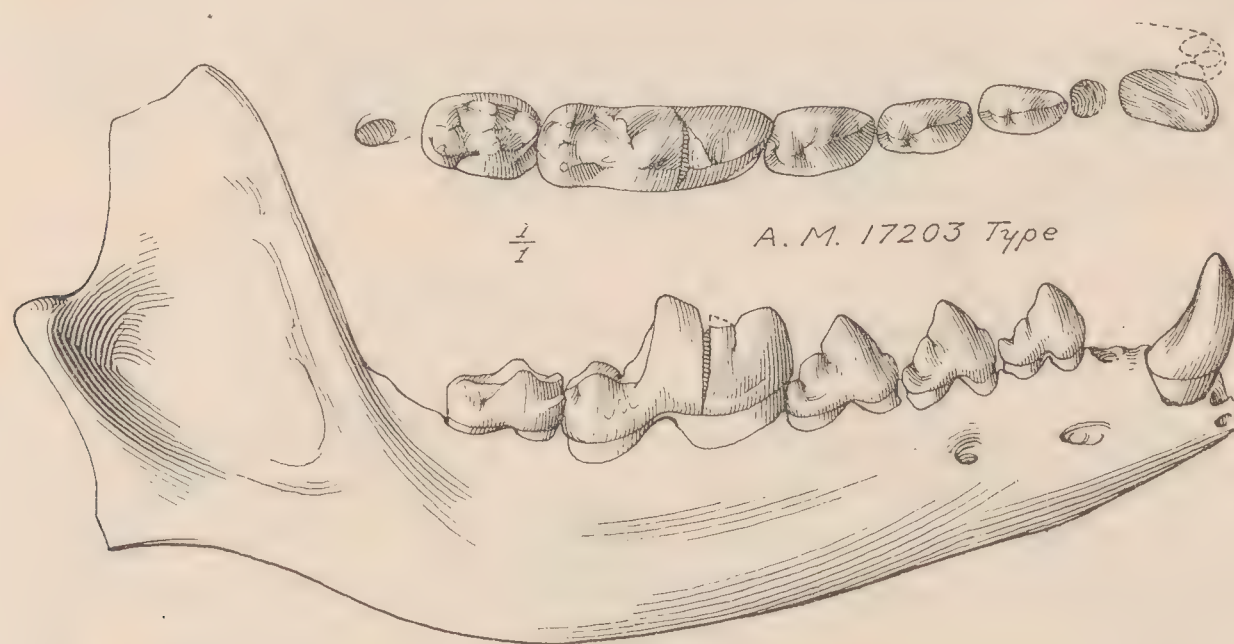


Fig. 1. *Tephrocyon confertus*, new species. Lower jaw, type specimen, external view with crown view of teeth; natural size. Snake Creek beds, expedition of 1916.

are available, *Nothocyon* Matthew, type *N. geismarianus* of the John Day,¹ and *Pseudocynodictis* Schlosser,² types *Canis gregarius* Cope, *lippincottianus* Cope, and *Cynodictis temnodon* Wortman and Matthew of the White River Oligocene. The European *Cynodictis*, as Père Chardin has clearly shown³ is not congeneric with the American Oligocene species which have been referred to it but covers a stage of evolution fairly intermediate between them and the Middle Eocene *Miacis*.

Leptocyon, new genus

Jaws slender, compressed, premolar region long, premolars spaced, compressed, with prominent accessory cusps. Heel of m_1 with low marginal entoconid crest obscurely divided into two cusps. Paraconid of m_2 low, vestigial, shelf-like. M_3 very small.

¹ *Hesperocyon* Scott, 1890, was presumably intended for the typical Canidæ of the John Day and antedates *Nothocyon*, but is a *nomen nudum*.

² Schlosser. 1902. Beitr. z. Kennt. d. Säug süddeut. Böhnerzen, Koken's Geol. u. Pal. Abh., V, Heft 3, p. 50.

³ Teilhard de Chardin. 1915. Ann. de Paléont., IX; Les Carnassiers des Phosphorites du Quercy, pp. 29-30.

Leptocyon vafer (Leidy)

Two lower jaws in the 1916 collection are referred to this species. The better one, No. 17201, shows p_4 to m_2 and alveoli of the remaining teeth; the second, No. 17202, has m_{1-2} complete.

Affinities. Although more progressive than *Tephrocyon* in the vestigial paraconid on m_2 the peculiar heel of m_1 does not suggest direct affinities to modern *Canis*. The proportions of the jaw show to an exaggerated degree the slenderness of the modern foxes especially some of the South American species. Although it parallels the foxes in this respect, yet both *Vulpes* and *Lagopus* appear to be too closely related in dentition to *Canis* to be separately descended from *Leptocyon* instead of *Tephrocyon*. Skulls, if known, would afford more decisive evidence.

Pliocyon, new genus

Dentition $\frac{3.1.4.2-3}{3.1.4.3}$. Tubercular dentition relatively large, carnassial teeth reduced, premolars much reduced, stout, short, canines and lateral incisors very large. Protocone of p^4 anterointernal, molars trigonal, wide transversely, conules small, not distinct; posterointernal shelf moderate. M_1 with distinct metaconid, broad heel, hypoconid crest submedian, entoconid a low internal shelf.

Whether this group of dogs deserves full generic separation from *Amphicyon* may appear open to question. The teeth are much as in *A. giganteus* save that the molars are less quadrate, m^3 is usually absent, the protocone of p^4 more anterior in position, and the inner halves of m^{1-2} more extended inward. It includes a group of species which have been commonly referred to *Amphicyon* by American authors, but Schlosser and other European authorities have always looked somewhat askance upon this procedure, and it has been generally recognized by my confrères here that the reference was questionable. The discovery of a well preserved skull in the Snake Creek beds enables me to define this American group more clearly and to determine its affinities more definitely.

Wortman in 1901¹ in describing *Amphicyon americanus* (Upper Miocene) expressed the opinion that it was a descendant of *Daphænus* of the White River Oligocene. Hatcher in 1902² adopted this view, and described as a new genus, *Proamphicyon*, a species from the White River admittedly closely related to *Daphænus* but considered as more directly ancestral to the American amphicyons. Matthew in 1903,³ while questioning this view of

¹ Wortman. 1901. Amer. Jour. Sc., II, pp. 200-204.

² Hatcher. 1902. Mem. Carn. Mus., I, pp. 65-108, Pl. xiv-xx.

³ Matthew. 1903. Science, XVII, p. 912; 1910, Bull. 361 U. S. G. S., p. 105.

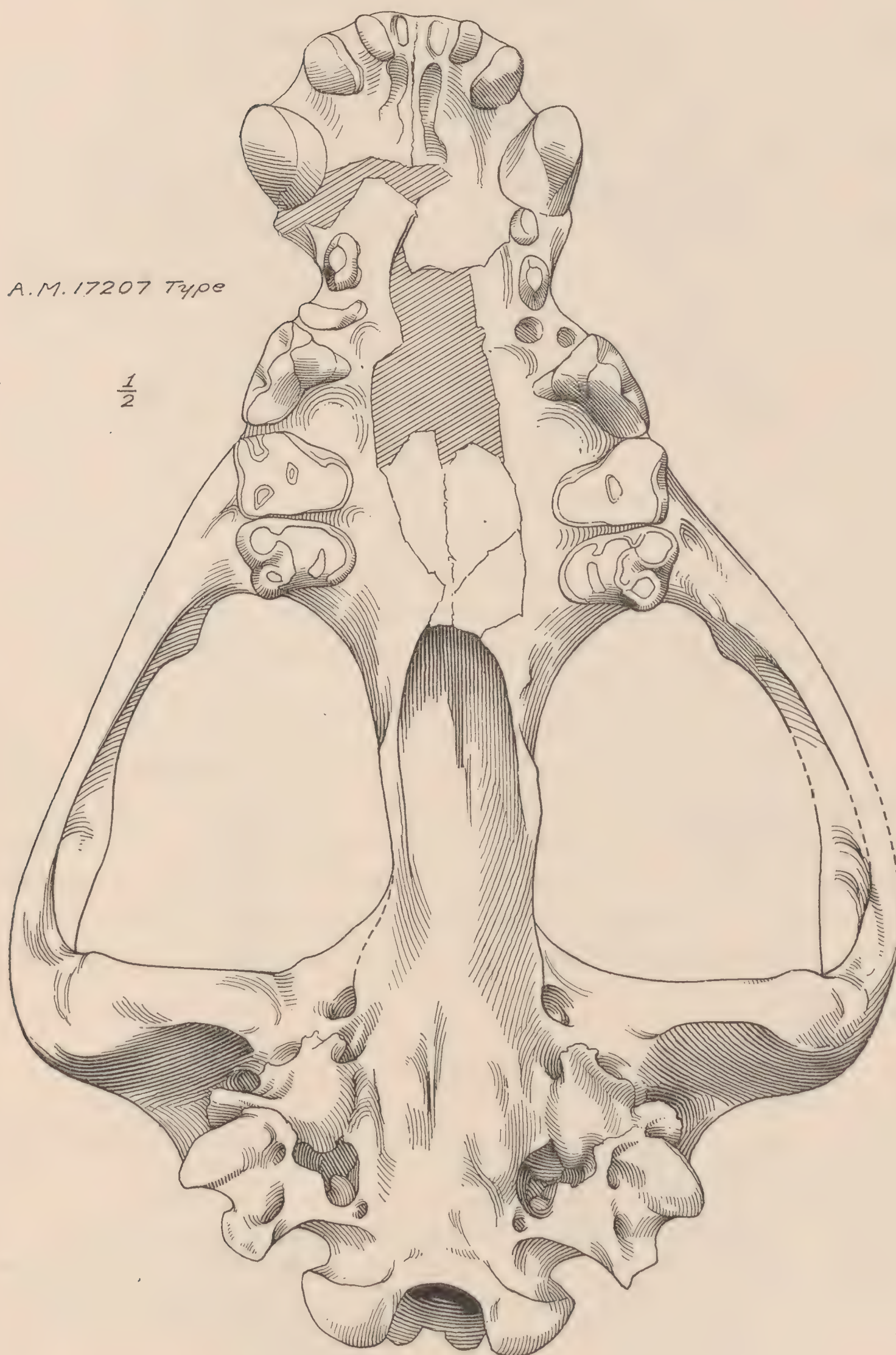


Fig. 2. *Pliocyon medius*, new genus, new species. Type skull, under side; half natural size. Snake Creek beds.

the phylogeny, regarded *Proamphicyon* as not generically separable from *Daphænus*. Peterson in 1910¹ also expressed the view that these American amphicyons are descended from *Daphænus* through *Daphænodon*, a new genus based upon a finely preserved skeleton from the Lower Miocene. Such, at least, I gather to be the substance of his opinion and quite agree with it, although I cannot see that the view affords any support to Hatcher's separation of *Daphænus* into three genera.² While it is quite possible that the three species upon which these three genera were based form the starting point for three important phyla, they are nevertheless closely allied species, separated by the usual amount of structural divergence that divides one canid species from another of the same genus. Only the most radical exponent of the phyletic view of classification — and Peterson is by no means such — should see in this a reason for reviving Hatcher's generic names. And a consistent application of the same view would necessarily make *Daphænodon* a synonym of one of Hatcher's "genera," *Proamphicyon*.

The only generic names which need to be considered for this American group are *Borophagus* Cope³ and *Borocyon* Peterson,⁴ both founded upon material in which I am quite unable to find any generic characters. Peterson cites as the generic characters of his genus some which are common to all or nearly all Canidæ while the others are common to several known genera. If topotypes are found, it may become possible to define it properly. It is from the Upper Harrison, a formation whose fauna has hardly any genera in common with the Snake Creek. It is therefore very improbable that it will prove to be identical with the present genus. *Borophagus* Cope is from the Blanco and must likewise await the discovery of topotypes before it can be validated. There are several distinct genera of large Canidæ or Ursidæ, described and undescribed, to any one of which it may prove to belong.

Pliocyon medius, new species

Size of "*Canis*" *ursinus* Cope, with which it may possibly prove identical, but exact comparisons cannot be made at present.

Size of skull about that of *Ursus arctos*.

M³ absent, m¹ and m² subequal, similar in proportions and construction. Premolars small, short, robust. P⁴ smaller in bulk than m¹, with small anteriorly placed internal cusp. P³ two-rooted, obliquely set in the jaw. P² somewhat smaller, two-rooted, not oblique. P¹ one-rooted. C¹ large, stout, prominent laterally but directed

¹Peterson. 1910. Mem. Carnegie Mus., IV, pp. 259-262.

²Peterson thinks that it does. See *loc. cit.*, p. 261.

³Cope. 1892. Amer. Nat., XXVI, p. 1028.

⁴Peterson. 1910. *Loc. cit.*, p. 263.



Fig. 3. *Pliocyon medius*. Upper teeth, natural size; and side view of skull, half natural size; type specimen, Snake Creek beds, expedition of 1916.

downward and somewhat forward. I^3 exceptionally large and stout. I^2 of more moderate size. I^1 smaller. Incisors set in a transverse row, not crowded. A short diastema between c^1 and i^3 ; no postcanine diastema.

Zygomatic arches stout and wide. Glenoid articulations large, postglenoid processes wide and moderately high, postglenoid foramen distinct. Tympanic comparatively small with a considerable bony meatus external to it. Mastoid process prominent, stout, constricted at base. Paroccipital process short spatulate, directed backward and very little downward. The base of the tympanic bulla is reflected at its anteroexternal margin over the back of the glenoid articulation from the postglenoid foramen nearly to the eustachian canal; and the mastoid border is similarly reflected over the posteroexternal margin of the bulla. Posterior lacerate foramen very large, oval, condylar foramen separate, small.

Palate extending only slightly behind m^2 ; pterygoid plates of palatines high, not approximated. Basicranial region wide, condyles large.

Occiput broad inferiorly with high occipital crest; sagittal crest high. Upper part of skull anteriorly unknown.

This species affords an interesting comparison with the Lower Miocene *Daphænodon*. The premolars are further reduced; the molars, especially m^2 , enlarged; m^3 lost; the incisors and canines enlarged; the arches much heavier and wider; the sagittal and occipital crests higher; the bulla more reduced; posterior lacerate foramen enlarged; mastoid process more prominent and robust — all characters showing a further progress on the lines of *Daphænus-Daphænodon*. Only in the paroccipital process is there a decided anomaly, for *P. medius* retains the primitive backward direction which is partly lost in *Daphænodon*¹ and is completely lost in the modern *Canis*.

Comparison with the European amphicyons is not possible as they are known only from fragmentary material, save for certain older species which are of doubtful reference to the genus and far more primitive than the present form. *Dinocyon thenardi* is still less known; "*D.*" *goriachensis* is removed by Schlosser to *Hemicyon* and is clearly much more bear-like in dentition, the molars more quadrate, the inner cusp of p^4 more median in position. Schlosser associates the typical *Dinocyon*, *D. thenardi*, with his cynodontine group, which would indicate that it differs from *Pliocyon* in the same way, provided it conforms to the diagnosis of the group.²

¹ If Peterson's figure is correct.

² The American genera placed by Schlosser (in Zittel's *Grundzuge der Palæontologie II Abth.*, *Vertebrata*, Revised Edition, 1911) in one or another of the canid "subfamilies" are very far from conforming to the diagnosis of the divisions to which they are assigned, and present, in fact, a very heterogeneous association. Any attempt at working out satisfactorily the phylogeny of the Canidæ and their relatives requires a far more intimate acquaintance with the American Oligocene, Miocene, and Pliocene species than has been displayed by any European writer.

Mustelidæ

Martes glareæ Sinclair

A lower jaw, No. 17208, agrees with Sinclair's type. It adds nothing of importance to the known characters of the species.

Brachypsalis modicus, new species

Type, a lower jaw, No. 17209, with canine and p_2 - m_1 r. and alveoli of the remaining teeth.

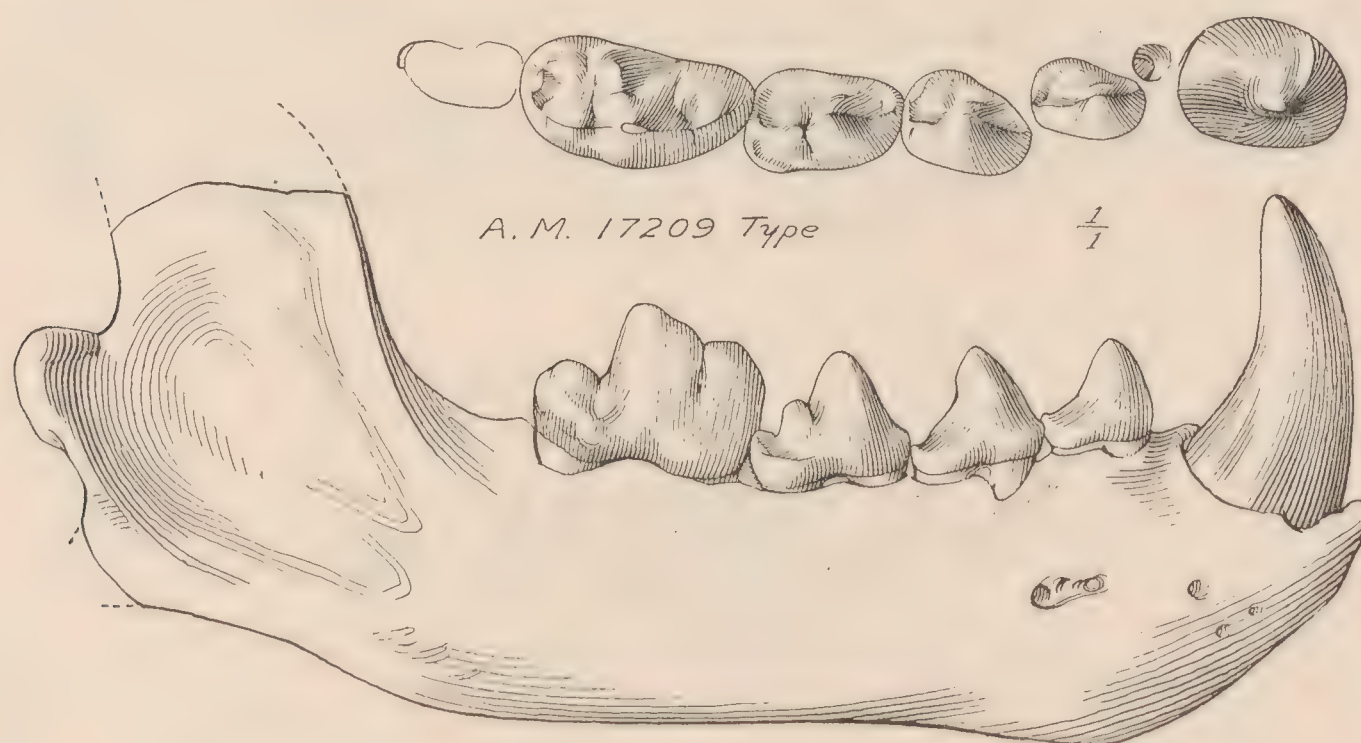


Fig. 4. *Brachypsalis modicus*, new species. Lower jaw, external view, and crown view of teeth; natural size. Snake Creek beds, expedition of 1916.

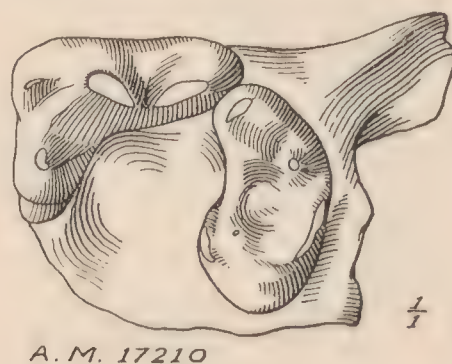


Fig. 5. *Brachypsalis modicus*. Fragment of upper jaw (topotype) referred to this species. Crown view, natural size, showing upper carnassial and first molar.

Distinguished from *B. pachycephalus* by more slender jaw, longer and much shallower beneath the molars, premolars less robust, m_1 smaller and more compressed, with smaller heel.

Part of an upper jaw, No. 17210, is provisionally referred to *B. modicus*. It differs from "*Æluroidon*" *hyænoides* Cope, which probably represents

the upper dentition of *Brachypsalis pachycephalus* or some related species, in the somewhat larger size of the molars, *pr.* and *pa.* of p^4 smaller, inner half of m^1 slightly broader, alveolus of m^2 apparently smaller.

Brachypsalis obliquidens Sinclair

This species differs from Cope's type of *B. pachycephalus* in an opposite sense from *B. modicus*. It is represented in our collection by No. 17211 and a few unnumbered fragments.

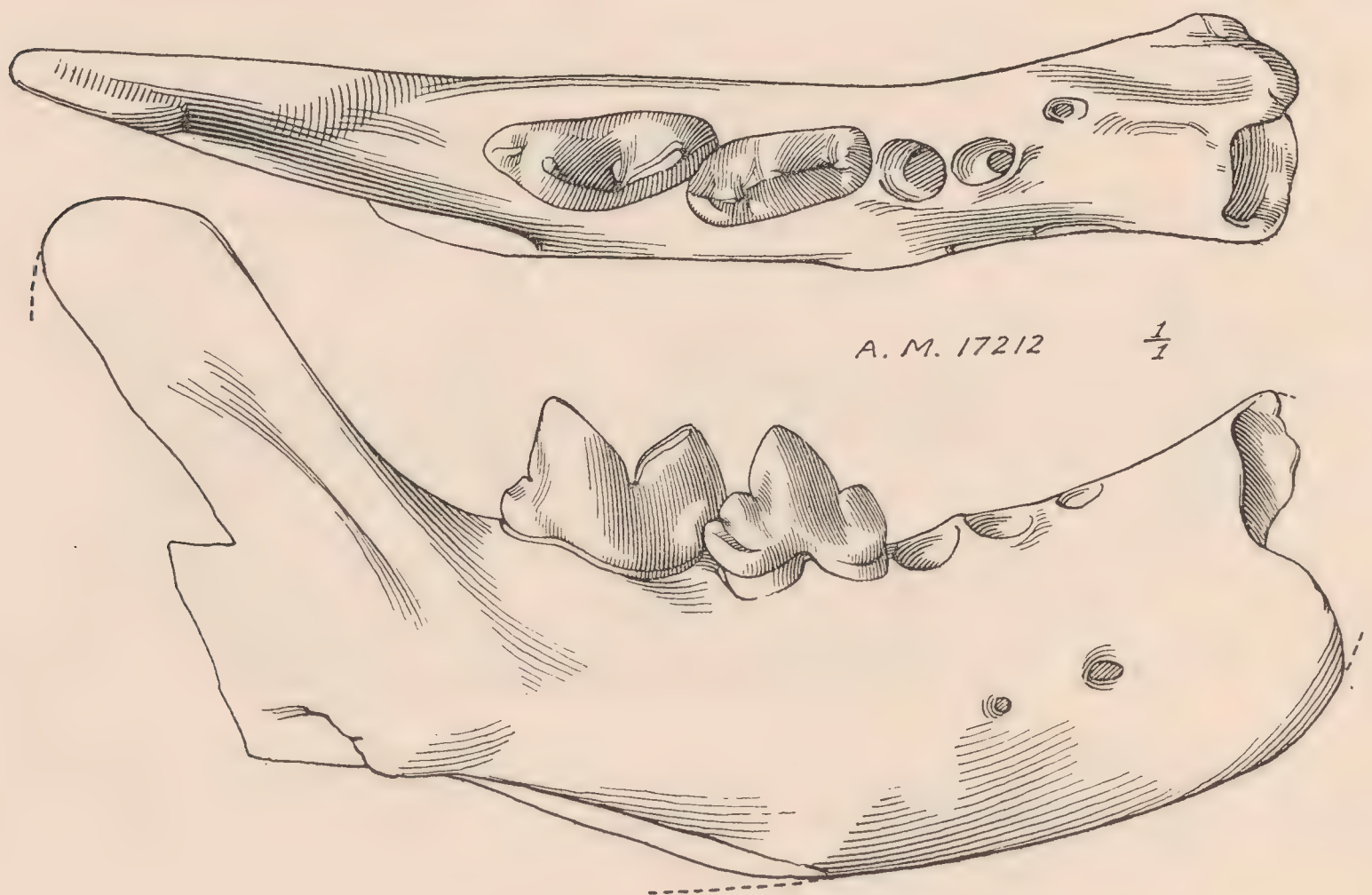


Fig. 6. *Pseudaelurus intrepidus sinclairi*, new subspecies. Lower jaw of type, superior and external views; natural size. Snake Creek beds, expedition of 1916.

Felidæ

Pseudaelurus intrepidus Leidy *sinclairi*, new variety

A lower jaw, No. 17212, is more complete than the specimen referred here by Sinclair and confirms the close relationship to Leidy's species. The most significant difference is the further reduction in the Snake Creek specimen of the vestigial metaconid and heel of m_1 , constituting a closer approach to true *Felis*. The size is somewhat smaller and the mental foramina somewhat more posteriorly placed, in both particulars agreeing with Sinclair's specimen.

RODENTIA

Castoridæ

Amblycastor, new genus¹

Large rodents apparently related to *Steneofiber* and *Euhapsis*, the cheek teeth of similar pattern so far as known, but relatively broader, p_4^4 relatively large, molars reduced and tending to become caducous. Incisor large, robust, with very convex anterior surface and numerous longitudinal grooves. Jaw extremely short and wide with very short diastema.

Amblycastor fluminis, new species

Type No. 17213, right lower jaw with p_4 complete, from Snake Creek beds, Lower Pliocene, 20 miles south of Agate, Sioux Co., Nebraska. Found by A. C. Whitford and George Stoll of the American Museum Expedition of 1916.

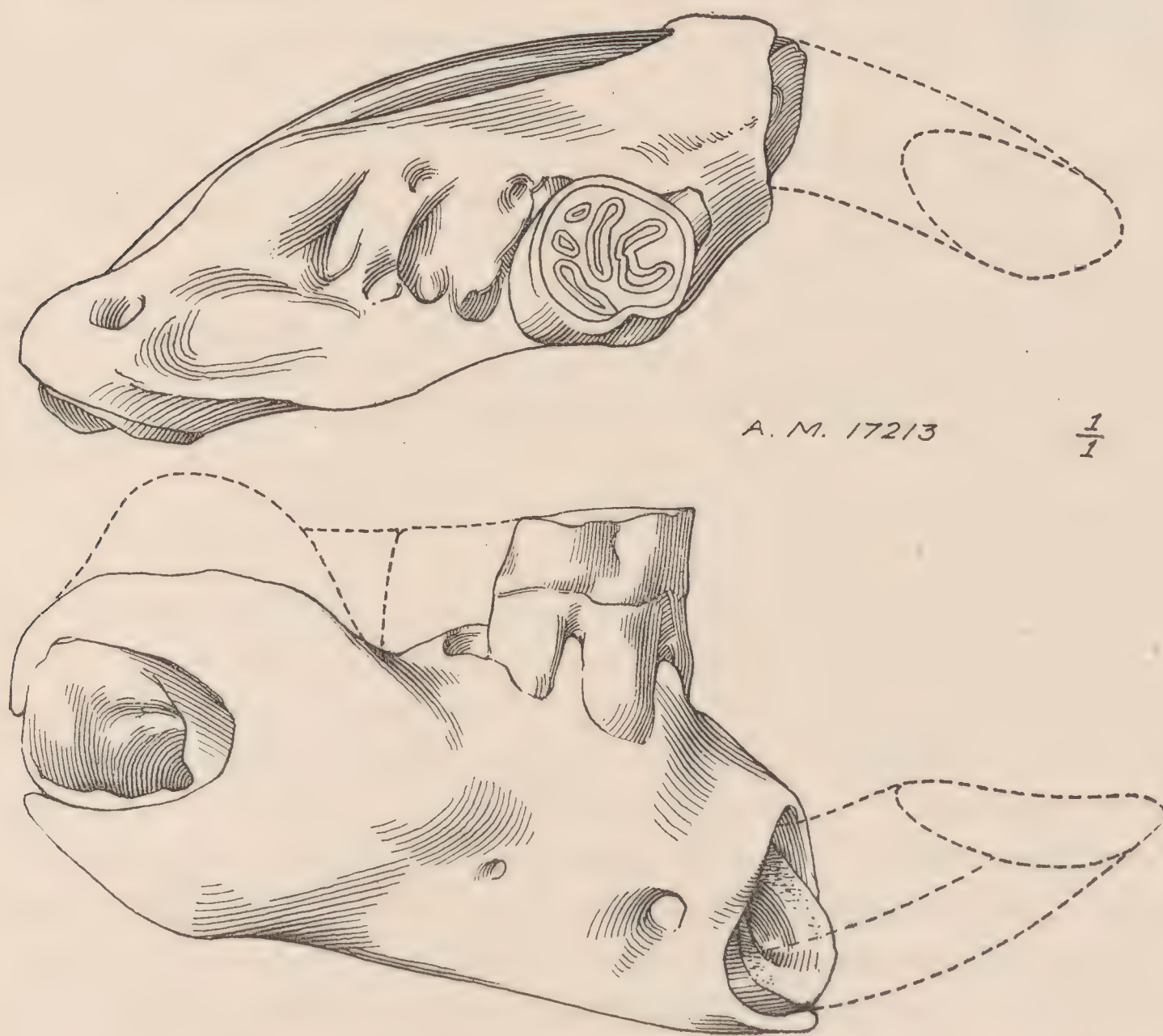


Fig. 7. *Amblycastor fluminis*, new genus, new species. Lower jaw of type, external and superior views; natural size. Snake Creek beds, expedition of 1916.

¹ Derivation: ἀμβλὺς, blunt, κάστωρ, beaver — in reference to the very short blunt muzzle, indicated by the proportions of the lower jaw.

The incisor is broken off at the alveolar border, and the back part of the jaw is broken away behind the posterior end of the incisor, the angle, condyle and coronoid processes missing and the specimen considerably waterworn. The posterior end of the symphyseal suture is preserved.

The premolar is 13 mm. long and 12 wide with a backwardly directed external inflection and four closed lakes similar in form and relations to the lakes in p_4 of *Euhapsis* at a corresponding stage of wear, and like them no doubt derivatives of the three internal inflections. The anterior lake is recurved to the form of a horseshoe with its ends pointing anterointernally, and occupies the anterior segment of the tooth. The median lake is transverse, extending from near the middle of the inner

border about two thirds across the tooth, and moderately concave anteriorly. The posterior pair of lakes are small, oval, lying between the end of the external inflection and the posterointernal border of the grinding surface.

The alveoli of the true molars have been partly closed and are further obscured by wear. The alveoli of m_1 and m_2 are still distinguishable as containing each an anterior and a posterior root, very wide transversely, the anterior root bifid; they are about as wide as the premolar but much shorter anteroposteriorly. The alveolus of m_3 is almost entirely closed, but the traces remaining indicate a smaller tooth.

The diastema is very short, only 9 millimetres on the specimen, but the bone may have extended further forward as a thin casing over the incisor. It extends downwards, inwards and forwards about equally from the anterointernal corner of p_4 .

The incisor is very stout, very convex on the anterior face so that its cross-section is a broad ovoid, wider anteriorly. It is rather sharply curved, the root appearing on the outer surface just posterior to m_3 . The enamel is heavily striated longitudinally.

The posterior end of the symphysis is opposite the middle of p_4 ; it is not extended downwards below the level of the incisive alveolus.

To this species should probably be referred the upper jaw fragment with p^4 - m^1 described and figured by Matthew and Cook under a provisional reference to *Hystriops venustus* Leidy. A reexamination of Leidy's type makes it appear improbable that it could belong to the same animal as the jaw here described. Its pattern approaches too closely to that of *Hystrix* and *Erethizon*, while in the new genus the correspondence in pattern of the premolars to *Steneofiber* almost certainly would involve a corresponding resemblance in the true molars. Moreover, I find it impossible to place the type tooth of *H. venustus* anywhere in the dentition of the present genus. It is not a premolar and is much too long and narrow for a true molar of *Amblycastor*.

Affinities. The animal is apparently a large and specialized descendant of the *Steneofiber-Euhapsis* group of the Lower Miocene. It parallels *Myla-*

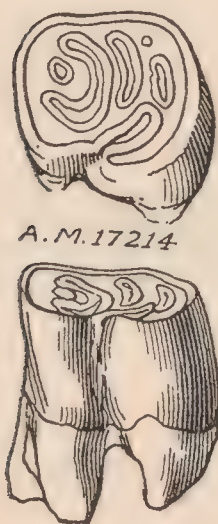


Fig. 8. *Amblycastor fluminis*. Lower premolar, p_4 of the left side, less worn than in the type specimen. Natural size, crown and external views. Topotype.

gaulus in the enlargement of $p\frac{4}{4}$ and reduction of the true molars, short wide jaw, etc., but it is not nearly related. It differs from *Eucastor* and *Castoroides* in these features, and the pattern of the grinding teeth shows little tendency to conversion into parallel oblique plates of enamel but, as in *Mylagaulus*, is converted by wear into a series of closed lakes, whose arrangement, however, is that of *Steneofiber* and wholly unlike that of the mylagaulids. The convex, striated enamel face of the incisor is not unlike *Castoroides* but the proportions of the jaw, pattern, and relative size of the grinding teeth forbid any closer affinity than a possible common descent from the Oligocene *Steneofibers*. Hystricomorph affinities are apparently excluded by the relations of the incisor to the axis of the jaw, which accord with those in *Steneofiber* and *Euhapsis*.

The genus is accordingly referred to the Castoridæ (*sensu lato*), its nearer affinities being with the group of species from the American Upper Oligocene and Lower Miocene referred to *Steneofiber*, and perhaps more especially to the genus *Euhapsis* closely related to this group.

It is the largest known rodent from North America, excepting *Castoroides*, and is exceeded in size only by the capybara among living members of the order.

PROBOSCIDEA

Sinclair has already called attention to the two types of *Mastodon* teeth found in the Snake Creek fauna. One is a zygalophodont type, allied presumably to *M. americanus*, the other a bunolophodont type of doubtful affinities.

The zygalophodont teeth are, however, quite as close to certain Miocene species as they are to *M. americanus* and intermediate between the two. The North American Miocene species of this group are

M. brevidens Cope. Type, m^3 ; Middle Miocene, Montana.

M. serridens Cope. Type, m^2 ; Lower Pliocene, Texas.

No additional material of *M. brevidens* is known. To *M. serridens* is referred a fine skull and jaws from the Clarendon of Texas found by J. W. Gidley and now in the American Museum. This specimen will be described later by Professor Osborn; it is here noted merely to point out that the species has much the characters and proportions of *M. productus*, the distinct type of teeth and straighter upper tusks being the most notable distinctions. As in all Miocene proboscideans one or more of the permanent premolars are functional. It could not be referred to the same genus as the American

mastodon. *Zygodolophodon* Vacek, 1877, type *Mastodon tapiroides* Cuvier,¹ appears to be available as a generic name for this group of species. The molars are distinguished from those of the *M. americanus-borsoni-progenium* group by the narrower proportions, with traces of subsidiary cusps appearing as ridges running downward and somewhat inward from the outer part of each transverse crest, and by the much more primitive condition of the tusks. The lower jaw is elongate with a pair of stout lower tusks; the upper tusks nearly straight with enamel band on outer side. P_{3-4}^{3-4} are functional teeth in the Lower Pliocene *Z. serridens*. I suspect that the later Pliocene species may have been more advanced than this, nearer to *M. americanus* in tusks and skull characters; but there is no adequate proof of this at present.

The Snake Creek species is very likely distinct from *M. serridens*, but until better material than isolated teeth is at hand it is not advisable to name it. I refer it therefore as *Zygodolophodon* aff. *serridens* (Cope).

A bunolophodont species also occurs in these beds but it does not appear possible to determine its affinities until better specimens are secured. The bunolophodont genera are

1. *Gomphotherium* Burmeister, 1837; type, *M. angustidens* Cuvier.²

Synonyms.—*Trilophodon* Falconer, 1842; type, *M. angustidens*.

Tetrabelodon Cope, 1884; type, *M. angustidens*.

?*Dibelodon* Cope, 1884, gen. indet.; type, *Mastodon shepardi* Leidy.³

Bunolophodon Vacek, 1877; type, *M. angustidens*.⁴

2. *Tetralophodon* Warren, 1852; species, *M. latidens* Clift, *M. arvernensis* Croiz. et Job., and *M. sivalensis* Cautley.

Synonym.—*Anancus* Aymard, 1855; type, *A. macroplus* = *M. arvernensis*.⁵

3. *Pentalophodon* Falconer, 1857; type, *M. sivalensis* Cautley.

4. *Rhyncotherium* Falconer, 1868; type, an unnamed Mexican species.

Beak of jaw sharply deflected; lower tusks present.

¹ The included species are *M. tapiroides*, *turicensis*, ?*pentelici*, and *borsoni*. The first is the earliest described, is first mentioned in Vacek's diagnosis of the group, and was apparently the species primarily in mind in distinguishing it. It is therefore selected as type. The type of *M. tapiroides* is a part of a molar from the Calcaire de Montabuzard near Orleans (Lower Miocene); Vacek figures a perfect second lower molar from Murinsel in Croatia which is very like our Snake Creek species.

² Type specified by Gloger, 1841, who misspells the name "*Gamphotherium*."

³ The type of *M. shepardi* is part of an upper tusk (in Amherst Museum) from Dry Creek, Stanislaus Co., Cal. In the original description the species is based solely upon this specimen; a tooth from another locality is mentioned but is referred to *M. obscurus*. The tusk has a strip of enamel, but is not further determinable.

⁴ The included species are *M. angustidens*, *longirostris*, *arvernensis*, *atticus*, and *pentelici*, of which *angustidens* is first mentioned and in other ways appears to be the proper lectotype species.

⁵ Auct. Lydekker. Brit. Mus. Cat. Foss. Mam. part iv.

5. *Stegomastodon* Pohlig, 1911; type, *M. mirificus* Leidy.

Synonym.—*Rhabdobunus* Hay, 1914¹; type, *M. mirificus*.

Some, if not all, of the South American species are probably referable to this genus.

6. { *Eubelodon* Barbour; type, *E. morrilli* Barbour.
 Megabelodon Barbour; type, *M. lulli* Barbour.²

PERISSODACTYLA

Rhinocerotidæ³

Three types of rhinoceroses occur in the American Pliocene; two of them, as yet, imperfectly known. They are:

1. *Teleoceras*. Mesaticephalic, nasals pointed, laterally compressed, with small median horn-core at tip; occiput subvertical, broad with wide

¹ It is most regrettable that the laws of priority require that Dr. Hay's name be set aside in favor of the one proposed by Pohlig in a short notice in the Bull. Soc. Geol. Belg. Pohlig's paper consists chiefly of a description of a lower jaw of the American mastodon in the Krantz collection, in which two small tusks are present, and an attempt to prove that this species is found only in the Tertiary of North America and did not survive to the Pleistocene. He appears to be very imperfectly acquainted with the considerable body of American literature on the lower tusks of *M. americanus*. Pohlig states that he has critically examined the evidence as to geological age in all the recorded occurrences of the mastodon in this country, and that none furnish any proof of post-Tertiary age; that the only occurrence in which there is any evidence as to geologic age is in the Charleston phosphate deposits, where the mastodon is associated with a Tertiary fauna. It is, of course, well known to most palæontologists that *Mastodon americanus* occurs only in interglacial or postglacial deposits in this country. It has never been found in any preglacial formation. As for the Charleston phosphates, it is equally well known that they are a mixed fauna in which the marine element is derived from two Tertiary horizons, while the terrestrial mammals are without any certain exception all Pleistocene. The mastodons there (*M. americanus* and *obscurus*) are accompanied by *Elephas primigenius*, *E. columbi*, *Equus* sp. div., and other well known Pleistocene types in abundance.

Pohlig finally refers to a mastodon tooth which he has seen in the collection of F. Krantz in Bonn and which had been identified as *M. mirificus*, and observes that this specimen has a certain amount of cement deposited in the valleys. This he believes is unique among mastodons, and proposes for this tooth the name of *Stegomastodon*. The presence of cement in the valleys of *Mastodon andium* teeth was recorded, however nearly a century ago, and has since been well known to European writers, and is noticed in European text-books.

Nevertheless, Pohlig's name must stand for the genus represented by "*Mastodon*" *mirificus*, of which a fine skull and jaws have been on exhibition for some fifteen years in the American Museum collection. The distinctive characters of the genus were pointed out by Hay when proposing his name *Rhabdobunus*. The lower incisors are absent; the molars are bunolophodont; m_3 , complex; m_{1-2} , early deciduous; the upper tusks curve upward and have no external enamel strip.

In this same short paper, Pohlig proposes another new Proboscidean genus, *Promastodon*, from the Puerco! of North America. Whether this is intended to be a new name for *Polymastodon*, together with a new view as to its affinities, is not clear; the name seems to be a *nomen nudum*.

² These genera represent a Pliocene stage of American mastodons corresponding in some respects to *Tetralophodon*, but distinguished by extreme length of the lower jaw. "*Mastodon*" *campester* Cope and *M. dinotherioides* Andrews fall into this group.

³ See Osborn's Revision of the Miocene Rhinoceroses in Bull. Amer. Mus. Nat. Hist., XX, 1904, pp. 307-326. Additional material from various formations leads to some modifications in Osborn's diagnoses and arrangement of the species.

vertex; upper incisors strong, lower tusks curving upward; premolars reduced, molars hypsodont. Lower limbs and feet very short.

2. *Aphelops*. Dolichocephalic, nasals long, pointed, not compressed, hornless or with rudimentary pair of horn-cores near tip; occiput vertical or backwardly projecting, narrow; upper incisors absent or weak, lower tusks heavy, procumbent; premolars unreduced, molars brachyodont. Lower limbs and feet rather long.

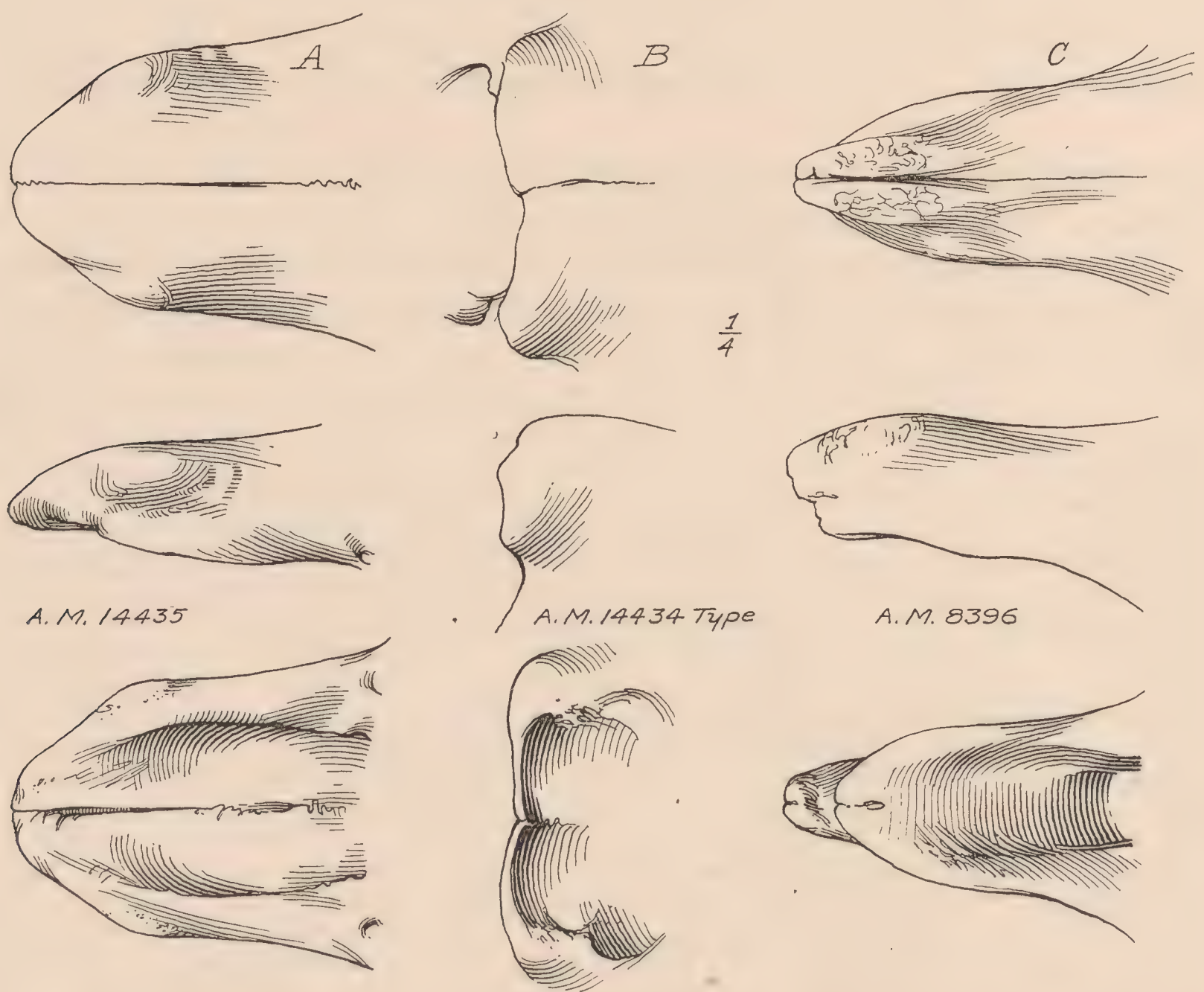


Fig. 9. Nasal bones of three American Pliocene rhinoceroses superior, lateral and inferior views: (A) *Aphelops* sp., cf. *ceratorhinus*; (B) *Peraceras troxelli*; (C) *Teleoceras fossiger*. All from Lower Pliocene of Nebraska and Kansas. One-fourth natural size.

3. *Peraceras*. Brachycephalic, nasals much abbreviated, square-ended, hornless; occiput pitched strongly forward, broad at base but much narrower at vertex; upper incisors absent; premolars unreduced, molars brachyodont. Lower jaws and skeleton not certainly known.

The first two of these genera are represented in the later Miocene (Pawnee Creek beds) by species of smaller size and more primitive characters, less differentiated one from the other than their Pliocene representatives.

These are *Aphelops megalodus* Cope and *Teleoceras medicornutus* Osborn, the latter including *Aphelops planiceps* Osborn and the specimens referred by Cope to *Aphelops crassus*. The ancestry of *Peraceras* is, as yet, unknown.

In the Snake Creek beds there are at least two distinct types of rhinoc-

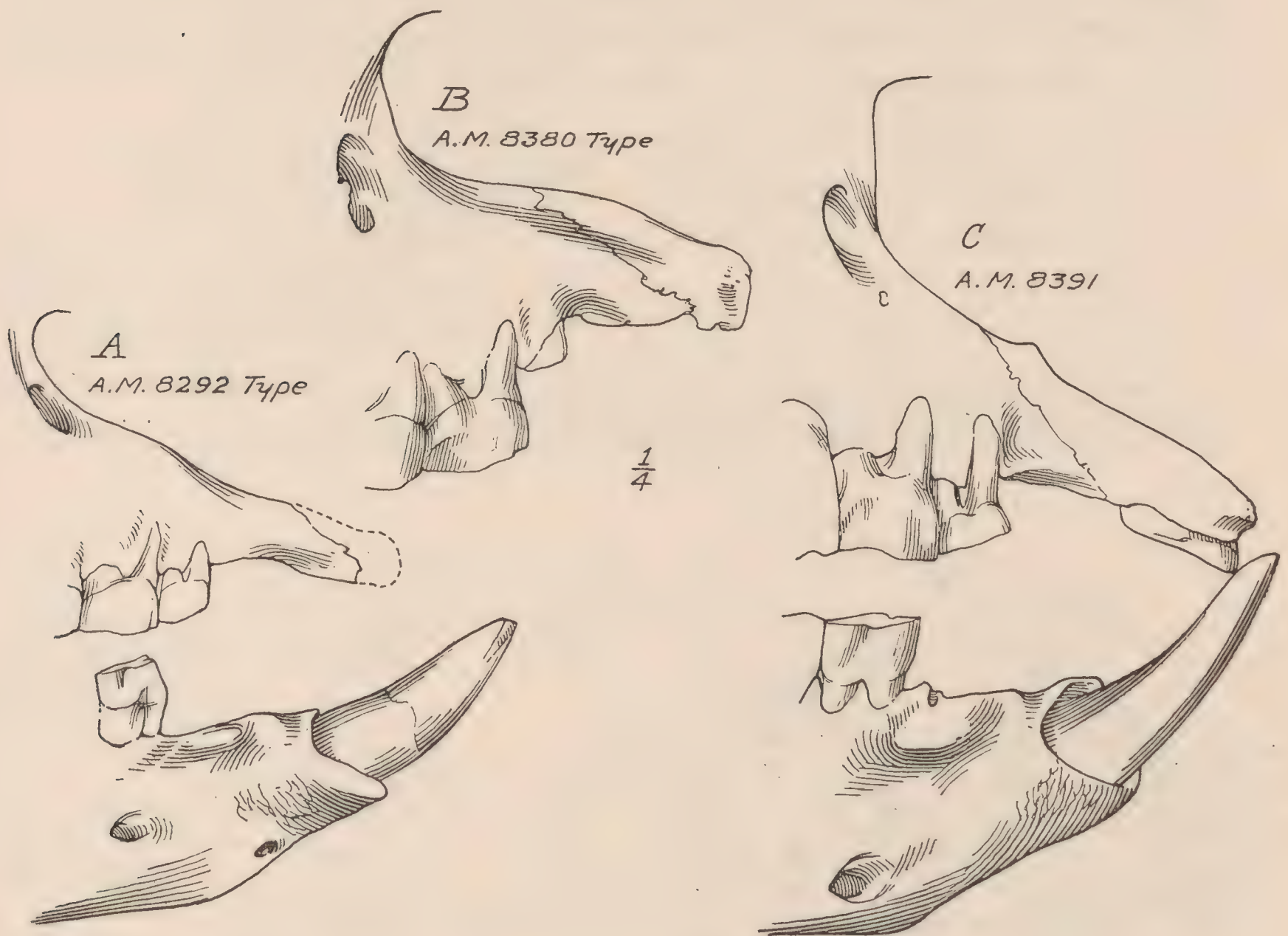


Fig. 10. Premaxillæ and tusks of *Aphelops*, *Peraceras*, and *Teleoceras*. (A) *A. megalodus*, Upper Miocene (Pawnee Creek beds) of Colorado; (B) *Peraceras superciliosus*, Lower Pliocene (Republican River beds) of Kansas; (C) *Teleoceras medicornutus*, Upper Miocene (Pawnee Creek beds) of Colorado. All one-fourth natural size.

ros, one a species of *Teleoceras*, the other apparently identifiable with *Aphelops crassus* Leidy (which, however, may be a species of *Peraceras*). *Peraceras* has not been recognized at the typical locality but a skull referable to it was secured some miles to the eastward in supposed Snake Creek beds. Very probably it is represented by some of the separate teeth of subbrachyodont rhinoceroses from the type locality, which are distinct from *A. crassus* but afford no reliable data for specific reference.

Aphelops Cope, 1874

Plates IV, V, and X

The type of this genus is *A. megalodus* from the Pawnee Creek beds of Colorado. A number of Lower Pliocene species of much larger size but with similar skull proportions, dentition, and, as it now appears probable, similar skeletal proportions have been referred to it. These are

<i>A. malacorhinus</i> Cope, 1881	Republican River, Neb.
<i>A. ceratorhinus</i> Douglass, 1903	Madison Valley, Mont.
<i>A. montanus</i> Douglass, 1909	Flint Creek, Mont.
? <i>A. crassus</i> (Leidy), 1858	Nebraska.
?? <i>A. meridianus</i> (Leidy), 1865	Texas and New Mexico.

The first three are based upon more or less complete skulls. The last two, based upon isolated and imperfect upper teeth, are provisionally

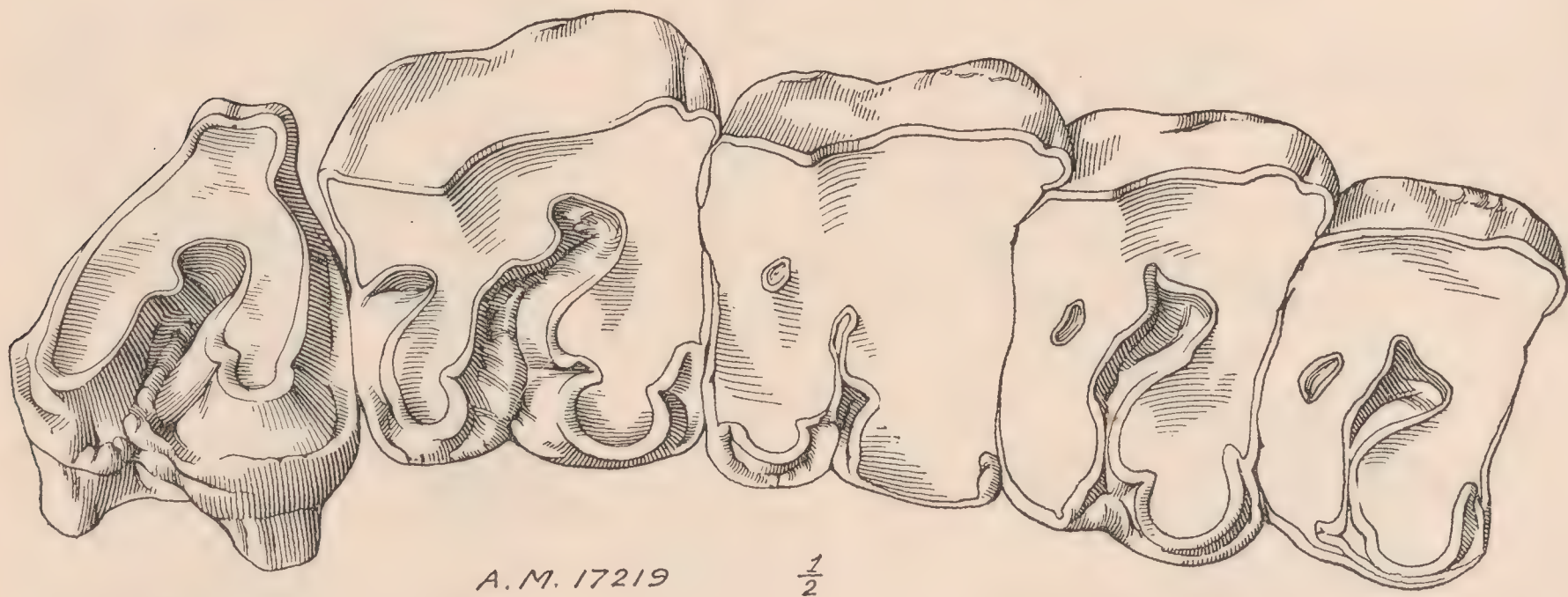


Fig. 11. *Aphelops crassus* Leidy. Upper teeth from Snake Creek beds referred to this species. Crown view, one-half natural size.

placed here upon the evidence of the referred specimens of *A. crassus*, described below, and the New Mexican specimen referred by Cope to *A. meridianus*. They are certainly not *Teleoceras*; but one or both may prove to belong to *Peraceras*.

? *Aphelops crassus* (Leidy, 1858)

Rhinoceros crassus Leidy, 1858, Proc. Acad. Nat. Sci. Phila., X, p. 28; 1869, Jour. Acad. Nat. Sci. Phila., VII, p. 228 (type limited to m³ and upper incisor), Pl. xxiii, fig. 8 [figs. 6-7?]; (*Aphelops*) Osborn, 1890, Bull. Mus. Comp. Zool., XX, p. 92 (last upper molar selected as type); (*Rhinoceros*), 1904, Bull. Amer. Mus. Nat. Hist., XX, p. 308 ("type and species indeterminate owing to uncertainty as to type").

Not *Aceratherium crassum* Cope, 1874, Ann. Rep. U. S. G. S. Terrs. for 1873, p. 521; nor of Leidy, 1869, *loc. cit.*, figs. 4-5.

In accord with the indications of Leidy, 1869, and Osborn, 1890, the last upper molar is the lectotype of this species. The other material associated with it as cotypes in Dr. Leidy's original description may not belong to the same species or genus, and I know of no evidence that any part belongs to the same individual.

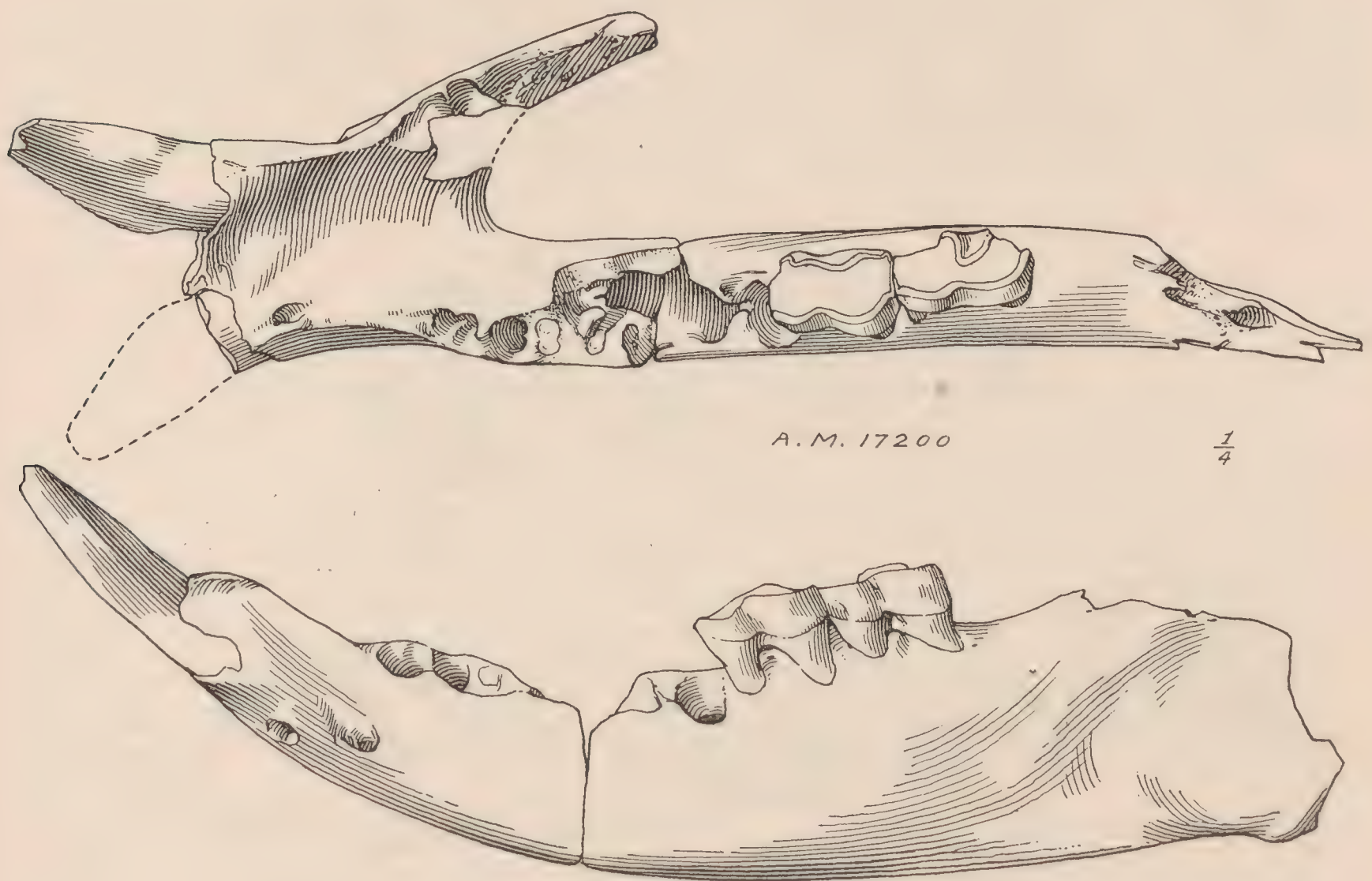


Fig. 12. *Aphelops* species. Lower jaw; one-fourth natural size. Snake Creek beds, expedition of 1916.

The type molar is considerably larger than *A. megalodus*, more triangular in form than *A. malacorhinus* or *Peraceras superciliosus*, and has a rather prominent crest at the bottom of the valley between protoloph and metaloph. This crest appears in a number of specimens from the Snake Creek beds which conform otherwise to the characters of the type and appears to be peculiar to the species. The specimens referred here, some of them provisionally, are as follows:

No. 17219, upper teeth, p^3 - m^3 r., p^3 and m^2 1.

13878, upper molar, m^2 r.

13879, upper molars, m^{2-3} 1.

13880, upper molar, m^1 r.

17222, upper and lower milk teeth, dp^{1-4} 1., dp^{2-4} r., dp_3 and m_1 1.
in parts of jaws.

17220, lower jaw, i_2 r., and m_{2-3} 1.

17220a, lower jaw, p_4-m_3 1.

" m_{1-3} 1.

The upper premolars are nearly as large as the molars, wide transversely, simple in construction, the crochet and antecrochet rudimentary. The molars are moderately brachyodont, crochet and antecrochet not strong, and crista not seen in any of our specimens. All of them show the sharp crest at the bottom of the median valley, merging into the base of the crochet externad and continuous with the inner cingulum internally.

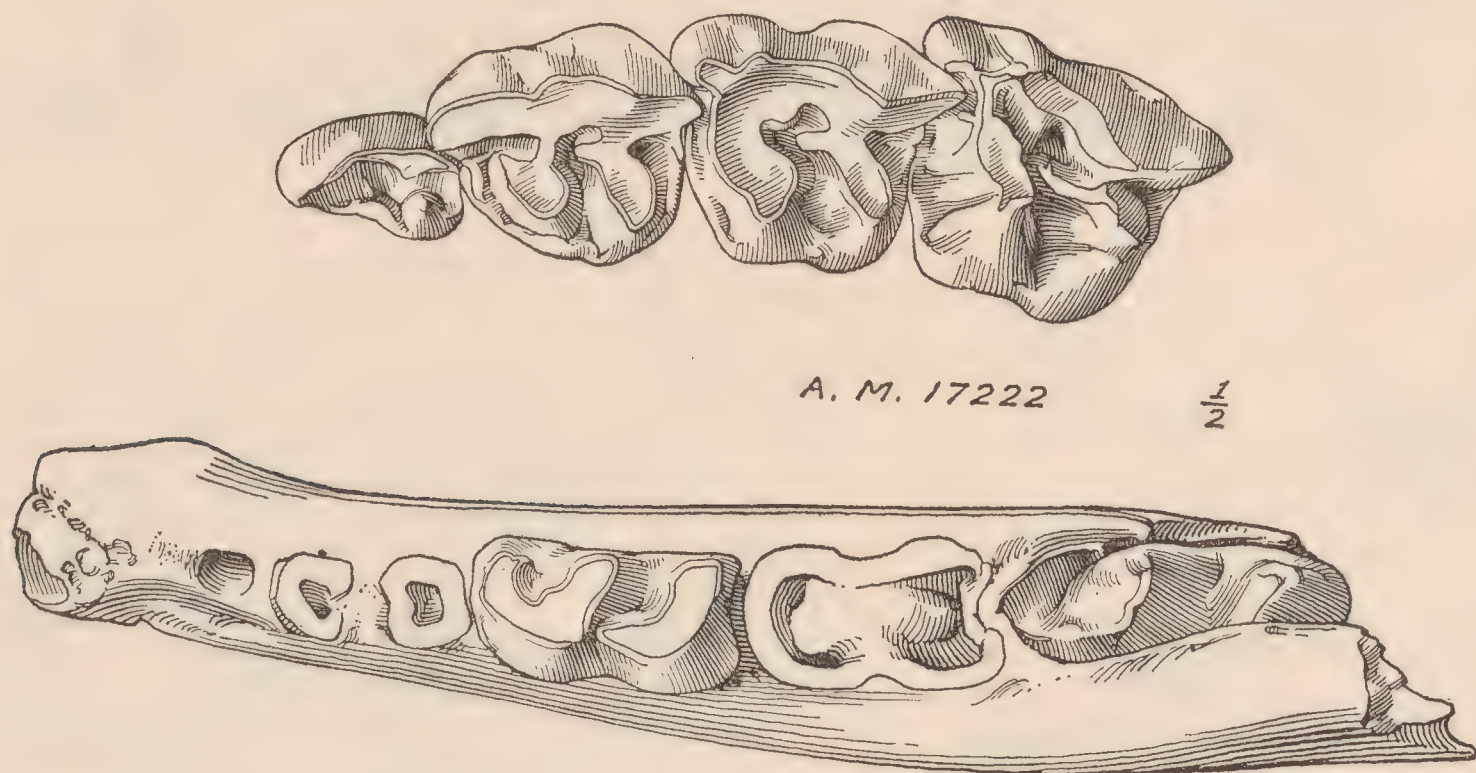


Fig. 13. *Aphelops* species. Upper milk premolars dp^{1-4} , and lower jaw of the same individual with the first molar partly erupted. One-half natural size. Snake Creek beds.

The lower jaws (provisionally referred, for they are not provably distinct from *Peraceras*) are rather shallow, less bowed inferiorly than in *Teleoceras*, and distinguished especially by the long flattened symphysis with heavy procumbent tusks, the brachyodont cheek teeth, unreduced premolars, and much smaller molars. They agree fairly well with the jaw of *A. ceratorhinus* Douglass but are of much smaller size than the jaw of a specimen (Amer. Mus. No. 9745) referred to that species.

The milk dentition is also readily distinguished from that of *Teleoceras*. Dp^1 is somewhat larger, with the inner crest of *T. fossiger* represented by two rudimentary cusps; dp^2 of about the same size but more triangular in outline, the protocone connected with the median instead of the anterior of the three crests that project inward from the ectoloph. Dp^3 and dp^4

are molariform, the former considerably smaller and more brachyodont, the latter only about two-thirds the size and very much shorter crowned than in *T. fossiger*. The crochets are decidedly weaker and the antecrochets quite rudimentary.

The lower milk molars are four in number instead of three as in *Teleoceras*. They are much narrower and lower crowned, especially the third and fourth, the crests more transverse.

The above differences are conformant with the differences in the permanent dentition between *Aphelops* (or *Peraceras*) and *Teleoceras*. The upper milk molar figured by Leidy as part of the type of *A. crassus*¹ appears to be a *Teleoceras*, and does not differ materially from *T. fossiger*. The lower milk molar, figured on the same plate,² I cannot positively identify.

Peraceras Cope, 1880

Type *P. superciliosus* Cope from Lower Pliocene of Nebraska.

Skull short, hornless with abbreviated nasals, premaxillæ vestigial, no incisors. Occiput strongly pitched forward, wide at base, narrowing towards vertex. Posttympanic process massive, flaring widely, separate from postglenoid process, which is also very robust and recurved forward. Paroccipital process attached at base to posttympanic, projecting downward, long and moderately heavy. Basioccipital with stout robust prominence for recti capitis muscles. Glenoid fossæ wide transversely; zygomatic arches wide and massive. Cheek teeth unreduced, premolars four, molars three, moderately brachyodont, p^{2-4} equalling m^{1-3} in size, p^1 small. Antecrochets rudimentary or absent, crochets moderate or weak, cristæ chiefly on premolars.

Lower jaw and skeleton unknown.

The cheek teeth of this genus are not readily distinguished from those of *Aphelops* of the *malacorhinus-ceratorhinus* group but the skull is widely different. The occiput in its strong forward pitch, narrow vertex and broad base, massive squamosal and occipital processes, etc. is very suggestive of *Rhinoceros indicus*; but the front part of the skull is very different, the posttympanic and postglenoid processes are separated, and the cheek teeth shorter crowned and more primitive in every way, the subordinate crests weaker and there is no suggestion of crenulation of the enamel.

Peraceras superciliosus Cope

Peraceras superciliosus Cope, 1880, Amer. Nat., XIV, p. 540; 1887, *idem.*, XXI, p. 1004, fig. 18; Osborn, 1904, Bull. Amer. Mus. Nat. Hist., XX, p. 312, figs. 6, 20, 21;

¹ Leidy, 1869, *loc. cit.*, Pl. xxiii, figs. 4-5.

² Leidy, *loc. cit.*, fig. 9.

Cope (Matthew), 1915, 'Hitherto Unpublished Plates of Tertiary Vertebrata,' Monograph Amer. Mus. Nat. Hist., Pl. CXLIV, CXLIVa, CXLIVb.

Type, Amer. Mus. No. 8380, a skull from the Republican River beds (Pliocene) of Nebraska.

A skull from supposedly Snake Creek beds west of Alliance, Neb., certainly belongs to this genus and may be provisionally referred to Cope's species. Some of the specimens referred to *Aphelops crassus* may also belong to *Peraceras*.

The skull, No. 17218, has the teeth more worn than in the type but agrees fairly well with it. The top of the skull is mostly destroyed by weathering, the under side well preserved. It shows the characteristic forward pitch of the occiput, massive recurved postglenoid process, thick and widely flaring posttympanic process, prominent thick knob at origin of recti capitis. It is somewhat larger than the type with broader and heavier zygomata.

Peraceras troxelli, new species

Plates VI-IX

Type, Amer. Mus. No. 14434, a skull from the Pliocene of Springview, Keyapaha Co., Nebraska. Found by E. L. Troxell 1916.

Smaller than *P. superciliosus*, nasals more reduced, cut short to the nareal notch above p^4 . Occiput narrower, occipital portion of cranium less sharply bent upwards. M^3 smaller, less quadrate, crochet somewhat more developed on premolars and molars. A small crista on m^2 .

The type skull was considerably broken up by weathering, when found, and many small pieces are missing, but it is undistorted by crushing and the outlines are practically complete save for the premaxillæ, which were not found. The anterior border of the nasals is complete and very peculiar in appearance; they appear as though cut squarely off just in advance of the lateral notch and do not project in advance of it as they do in *P. superciliosus*. The molars are moderately high crowned, p^{2-4} about the same size as m^{1-3} , p^{-1} small, not preserved. The third molar is only slightly squared at the base; the crochet is prominent on m^{1-3} ; antecrochet rudimentary and confined to the base of the protoloph; crista absent, except on m^2 of one side; p^{3-4} have crochet and crista united, enclosing a medifossette; strong basal cingulum around inner, posterior, and anterior faces, so that in much worn teeth the pre- and postfossettes would also be distinct. On p^2 the antecrochet tends to unite with the metaloph to enclose a prefossette; the crochet is strong, united to the crista on p^2 l. but not on p^2 r.; and the internal cingulum is deeply notched and almost discontinuous at the median

valley. The molar cingula are discontinuous internal to the protocones, notched at the median valley.

Minor differences in many points between right and left teeth of the type individual show that too much weight should not be assigned to the details of cusp construction as species characters.

Teleoceras Hatcher

Type, *T. major* Hatcher = *Aphelops fossiger* ? Cope.

Skull of moderate length; nasals somewhat shortened, pointed, and pinched in toward the tip, with a small median terminal horn on upper surface, more or less distinctly indicated (apparently according to sex). Zygomatic arches moderately heavy, narrow anteriorly, broadened posteriorly. Occiput subvertical, broad, quadrate, the vertex very wide. Postglenoid process rather slender, posttympanic process thin, plate-like, plastered to lambdoid crest, and not freely projecting.

Upper incisors well developed, lower incisor tusks recurved upward, symphysis and diastema short. Lower premolars reduced in size and usually in number, $\frac{4-3}{3-2}$ in adult. Milk premolars, $\frac{4}{3}$. Molars large, hypsodont; crochet, antecrochet, and crista strong, and cingula high on upper molars; the half-worn teeth usually with three enclosed fossettes. The molar series considerably exceeds the premolar series in size in upper or lower cheek teeth.

Lower limb bones and foot bones very short and small in comparison with bulk of body. See Plates IV and V.

Osborn¹ admits *T. major* as doubtfully distinct from *T. fossiger* on the ground of larger size and describes *T. medicornutus*, a species clearly distinct and more primitive in skull form. The type of *medicornutus* is from beds 15 miles northeast of Grover, Colorado, which are of doubtful correlation. The paratype, however, Amer. Mus. No. 9374, is from typical Pawnee Creek beds, and it is represented also by a number of incomplete skulls, jaws, and skeleton parts in the American Museum collection from this formation. *Aphelops planiceps* Osborn, 1904, was based upon a skull lacking the front part, and belongs, I believe certainly, to the same genus as *T. medicornutus* and quite probably to the same species. The specimens which Cope referred to *A. crassus* Leidy in 1874 also belong to this species, also the front part of a skull, No. 9375, with the incisors and cheek teeth and one nasal preserved.

The cervicals, end of ulna and certain of the fore foot bones figured by Cope (Matthew) 1915² belong with parts of a skull of this species, although

¹ Osborn. 1904. Bull. Amer. Mus. Nat. Hist., XX, p. 314.

² 'Hitherto Unpublished Plates of Tertiary Vertebrata,' Monograph Amer. Mus. Nat. Hist., Pl. CXXIX, figs. 1-7, Pl. CXXX, figs. 1-3.

through an error in the records they were supposed to belong to the type and paratype of *Aphelops megalodus*. See Plate X.

T. medicornutus is considerably smaller than *T. fossiger* and more primitive in various respects. The nasals, however, are distinctly of the *Teleoceras* type, as are also the occiput, the cheek teeth, the upper and lower incisors, the cervicals, the short legs, and feet. It may be regarded as intermediate between the European Lower Miocene "*Teleoceras*" (*Brachypotherium*) *aurelianense*¹ and the highly specialized *T. fossiger*.

In the Snake Creek beds a species occurs which appears to be slightly

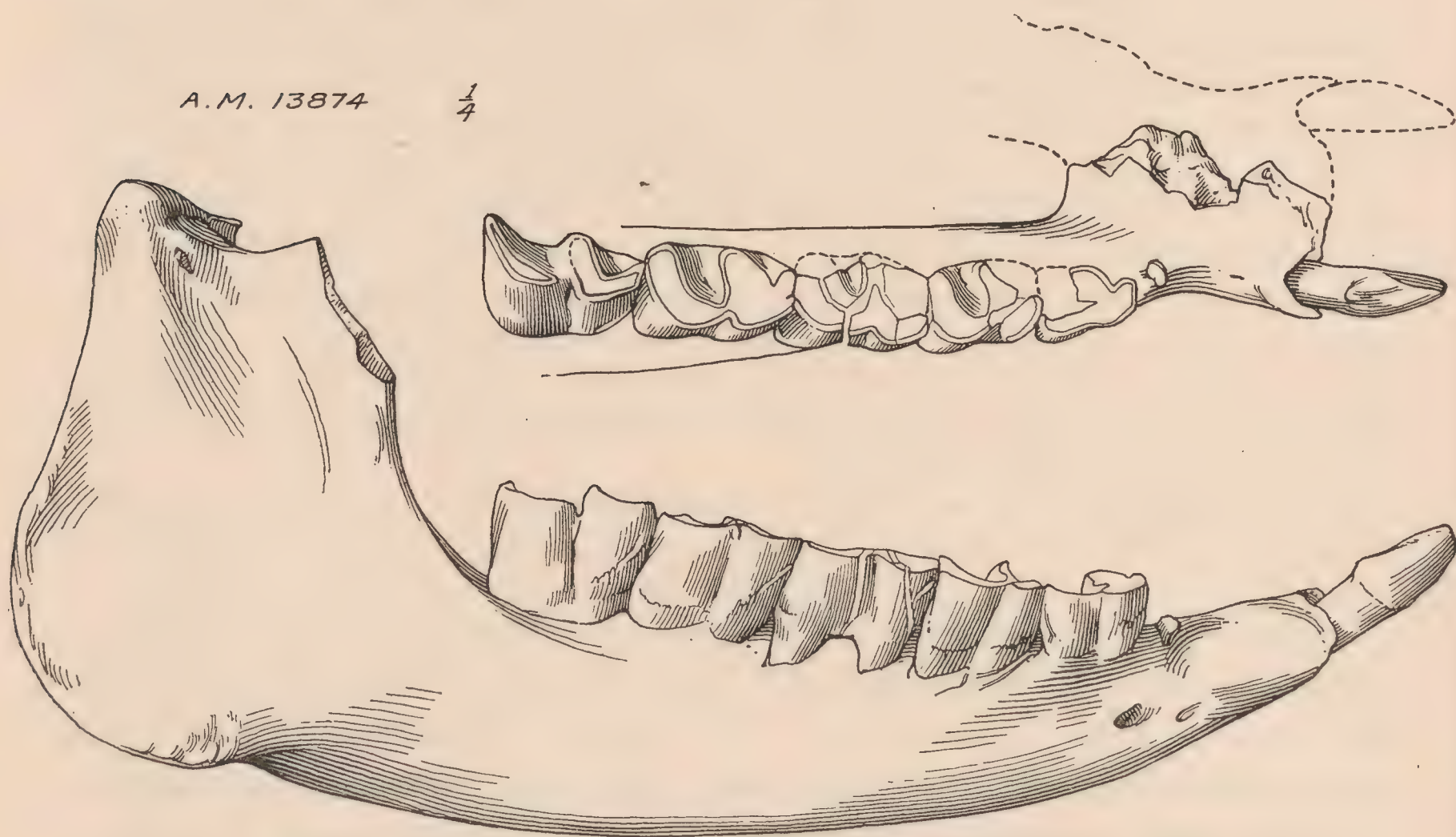


Fig. 14. *Teleoceras* species. Lower jaw; one-fourth natural size. Snake Creek beds, expedition of 1908.

more primitive in some respects than *T. medicornutus* although it may, when better known, prove to be more progressive in other features. We have no better specimens than lower jaws and fragments of the skull and various limb and foot bones. Pending the securing of more complete specimens, it appears better not to give a specific name.

¹ M. Repelin (Repelin, 1917. Ann. Mus. Hist. Nat. Marseilles, XVI, pp. 1-47, Pl. I-XVI) has recently described and figured a series of admirable specimens from the upper Oligocene of France under the name of *Teleoceras aginensis*. While these are evidently related to "*T.*" *aurelianensis*, they are clearly not congeneric with *T. fossiger*. This European group may perhaps be ancestral to *Teleoceras*.

Teleoceras sp.

The best specimen is No. 13874, a lower jaw from the Snake Creek beds, 23 miles south of Agate, Neb. It is smaller than *T. medicornutus*, with decidedly smaller tusk; p_1 present, although very small. The teeth are well worn, the molars large and hypsodont, premolars reduced, symphysis short, lower tusk upward curving; these characters place it in *Teleoceras* but it is much smaller and more primitive than *T. fossiger*. A number of teeth, and skull and skeleton parts are referable to this genus and probably to the same species. One shows the characteristic nasal with its rudimentary horn; various foot bones also show the generic characters, but all of them indicate a smaller and less specialized species than *T. fossiger*.

Equidæ

Six genera are represented: *Parahippus*, *Hypohippus*, *Merychippus*, *Hipparion*, *Protohippus*, and *Pliohippus*. The first two are scarce; the third occurs in overwhelming abundance in most of the pockets; the fourth is almost as abundant in certain pockets; the last two are also common in certain pockets. Thus far, no skulls or skeletons have been obtained except one of *Pliohippus* found by H. J. Cook, but numerous upper or lower jaws and vast numbers of separate teeth.

Parahippus

There is evidence of but one species, which is not separable from *P. cognatus* Leidy. The permanent upper and lower teeth show a medium-sized, moderately progressive species with a little cement in the valleys and slopes of the cusps, but not enough to fill them until the teeth are nearly worn down. The foot bones have not been identified.

Hypohippus

This genus is even scarcer than *Parahippus* but apparently two species are present, one of which may be *H. affinis* Leidy; the other, *H. pertinax*, is of smaller size, approximately equal to *P. cognatus*.

Hypohippus pertinax, new species

Type No. 17232, lower jaw with p_1 – m_3 . Size of *H. equinus*; p_1 minute, vestigial; p_2 broader, heel of m_3 smaller than in Scott's species.

Merychippus

Numerous upper and lower jaws, pieces of jaws and thousands of isolated teeth are found, this being by far the most abundant genus in the fauna. The majority fall into a group representing either one species very variable in size and somewhat variable in length of crown, pattern etc., or else a number of closely allied species not separable by the teeth alone. This species or group approaches *Hipparion* in the separation of the protocone nearly to the base, but the teeth are shorter-crowned, and the milk teeth are the characteristic wide, brachyodont, imperfectly cemented type of *Merychippus*. The protocone is rounded but with the characteristic crest on its buccal side reaching out toward the protoconule crescent and joining it near the base. The parastyle is not so broad as in *Hipparion*; the mesostyle, broad at the base, narrows rapidly to a thin crest, while in *Hipparion*, *Protohippus* and *Pliohippus* it holds its width further up on the crown — up to the top in *Equus*. The caballine fold is present; the two primary folds projecting into the anterior lake and the one primary fold projecting into the posterior lake are present, with a few minor folds which disappear towards the top and bottom of the crescents.¹

The *Merychippus calamarius* group

I refer this very abundant group to Cope's species from the Santa Fe beds of New Mexico, although most of the material is smaller and somewhat shorter crowned.

The *Merychippus insignis* group

Another common form has smaller, decidedly shorter-crowned teeth with somewhat more simple construction, but is otherwise nearly related to *M. calamarius*. The milk teeth agree closely with those of *M. insignis*; the permanent teeth are not easily separable from *M. severus* and other ill-defined species of the Middle Miocene.

Merychippus patruus Osborn *obliquus*, new variety

Many teeth in the collection belong to the *M. sejunctus* group which is allied to *Protohippus* and *Pliohippus* and distinguished by closer union of

¹ I state this construction in terms of the enamel surface of the tooth, as observed in preformed teeth that have not yet received their coating of cement. The customary method of comparing equine teeth by the pattern of the wearing surfaces of the crowns, although necessary when material is scanty, gives a very imperfect notion of the real construction and is a principal cause of the confusion in their affinities and phylogeny.

the protoconule crescent with the protocone and imperfect union of protoconule with metaloph, amounting sometimes to complete separation. (*M. insignis* displays this also in some degree.) These pass insensibly through numerous intermediate stages into these more progressive genera. Whether these stages represent primitive survivals, hybridism, or individual variation, I am not able to determine. No other collections afford such quantities of material for comparison, and it may be that the apparent distinctness of equine species elsewhere is due to insufficient material for examination. But it is also possible that the Snake Creek pockets represent a considerable lapse of time, and, until the pockets have been separately exploited and carefully compared, we may suppose that we have to do with successive stages in the evolution of a phylum, tangled up with variation and hybridism.

The *Protohippus perditus* group

Jaw fragments and teeth agreeing fairly well with Leidy's type are not rare but no good specimens have yet been secured.

The *Protohippus placidus* group

Incomplete jaws and rather numerous teeth of the type represented by Leidy's *placidus*, but many of smaller size, more hypsodont. Better material is necessary to clear up their precise relations.

The *Hipparion gratum* group

Jaw fragments and teeth, of which some agree well with *H. gratum*, while others are in varying degree smaller and longer crowned, some molars as hypsodont as *Equus*, but the area of the crown at the base scarcely exceeding that in *Mesohippus bairdii*. These teeth are parallel to the series referred to *Protohippus placidus* and are nearly related, if one may judge from the similarity in details of construction; but the two series do not grade into each other. Certain species from the Pliocene of Mexico and Florida belong to this group, but none are so extreme as some of our Snake Creek teeth. *H. lenticulare* of Texas also belongs here.

The *Hipparion occidentale* group

Larger species with a marked tendency to flattening of the protocone heavy mesostyle, usually much complexity in the infoldings of the enamel borders of the fœssettes.

Very numerous teeth and a few jaw fragments represent this group, most of them belonging to a form smaller than *H. occidentale* proper, but not agreeing with any of the later described "species." The protocone is frequently round-oval towards the top of the crown although flattened-oval towards the base; complexity of enamel foldings extremely variable.

The *Plihippus mirabilis* group

Jaws and jaw fragments and numerous teeth agree with *P. mirabilis* Leidy or with the doubtfully separable variants *P. supremus*, *pernix*, *robustus*, etc. All lie on the boundary between *Protohippus* and *Plihippus*, and are rather nearly related to the *Protohippus perditus* group, but not to the *P. placidus* group. Larger size, somewhat shorter and more curved upper molars, fossettes broader with simpler enamel borders, are the chief distinctions from the *perditus* group.

The *Plihippus spectans* group

These are not as common as the small Plihippi but fortunately a complete skeleton has been discovered so that the characters can be fully understood.

P. spectans, *interpolatus*, *lullianus*, etc., are probably all monodactyl, the skull large and elongate, limbs and feet of moderately slender proportions; teeth large and decidedly more hypsodont with less curvature in upper molars than in the smaller group. Protocone more or less flattened, union with crescent less complete than in *P. mirabilis* group, mesostyle heavy, enamel borders simple.

ARTIODACTYLA

Dicotylidæ (= Tagassuidæ)

There are two distinct species of peccary in the Snake Creek. One is very close to Cope's *Prosthennops serus*; it has more bunodont teeth and p_4 fully molariform. In the other, the teeth are somewhat lophodont and p_{3-4} imperfectly molariform. The latter is very close to the modern *Dicotyles* in teeth; it may, however, be *P. crassigenis* Gidley, which is quite distinct from *Dicotyles* in the skull. Until better material is available, both species are referred to *Prosthennops*.

Prosthennops serus Cope

No. 17310, lower jaw with unworn p_4 - m_3 is referred here. Various teeth in the 1908 collection belong to this and the following.

? *Prosthennops* cf. *crassigenis* Gidley

A lower jaw in the 1908 collection, No. 14052, is provisionally referable.

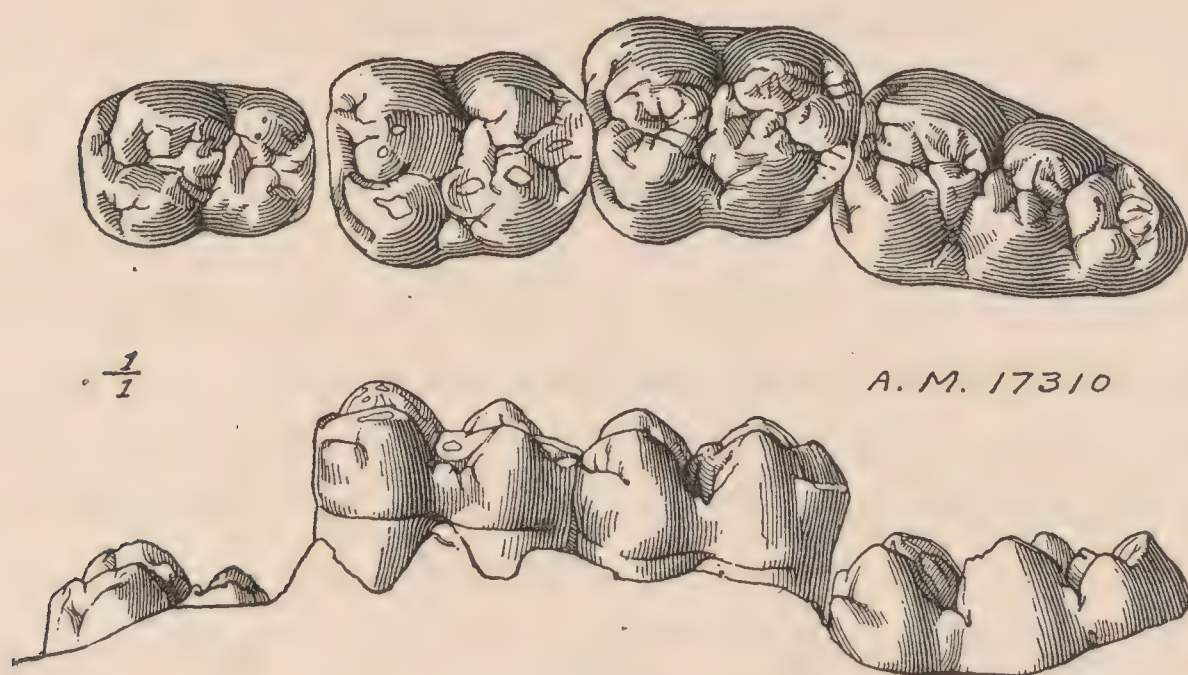


Fig. 15. *Prosthennops serus* Cope. Unworn lower teeth p_4 - m_3 in fragment of jaw from Snake Creek beds referred to this species. Natural size; crown and external views.

Oreodontidæ¹*Metoreodon* Matthew and Cook

This genus is most readily distinguished from *Merychys* by the characters of the premolars. The skull is not known in either genus,² for the skulls referred to *Merychys* from the Lower Miocene, *M. arenarius*, *minimus*, etc., are probably not of this genus; they differ very considerably from the Middle Miocene (Pawnee Creek) skulls which have been referred to *M. elegans* but are also of doubtful reference even generically; and no skulls of *Merychys* from the *Hipparion* zone, to which the types of the genus belong, have yet been found.

The teeth differ in the following features.

Upper premolars p^1 , p^2 , and p^3 broader and more crowded than in *Mery-*

¹ = Agriochoeridæ or Merycoidodontidæ.

² Since these lines were written, Barbour and Cook have published a description and figure of a skull of *Metoreodon*.

chyus; with a distinct isolated anterointernal tubercle, absent in *Merychys*; the transverse crests of p^1 more developed, but the median transverse crest of p^2 and p^3 more rudimentary. Lower premolars, p_2 , p_3 , and p_4 , with an anterior transverse crest extending towards the inner side, absent in *Merychys*. External valleys of lower premolars more distinct. Molars very similar in the two genera.

Metoreodon relictus

No. 17311, a palate and lower jaws is referred here.

Camelidæ

Next to Equidæ, Camelidæ are the most abundant fossils in the Snake Creek fauna. The following genera are represented.

Protolabis Cope. Three upper incisors, the first two usually small. Cheek teeth moderately hypsodont; cheek premolars $\frac{3}{3}$, moderately reduced.

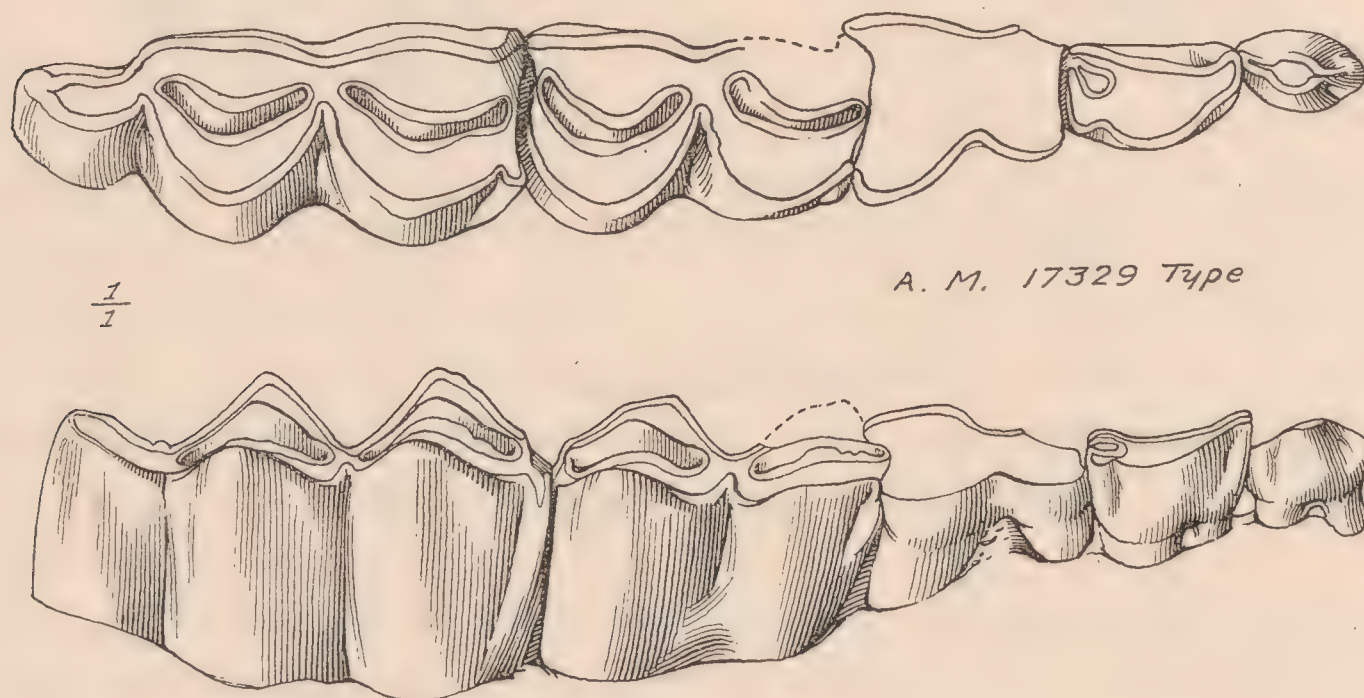


Fig. 16. *Plianchenia singularis*, new species. Teeth of type lower jaw, crown and external views; natural size. Snake Creek beds, expedition of 1916.

Limb bones relatively small, rather short, metacarpals separate or imperfectly united.

Procamelus Leidy. One upper incisor. Cheek teeth more hypsodont; cheek premolars $\frac{3}{3}$, considerably reduced. Limb bones relatively small, moderately long, metapodials fully united.

Alticamelus Matthew. One upper incisor. Cheek teeth more or less hypsodont; cheek premolars $\frac{3}{3}$, unreduced. Limbs and feet relatively large, much elongate, metapodials fully united.

Pliauchenia Cope. One upper incisor. Cheek teeth subbrachyodont to hypsodont; cheek premolars $\frac{3}{2}$, reduced much as in *Procamelus*. Skeleton unknown.

Megatylopus Matthew and Cook (subgenus of *Pliauchenia*). One upper incisor. Cheek teeth more or less hypsodont; cheek premolars $\frac{2}{2}$, much reduced. Limbs moderately large, very massive. All gigantic species. Phalanges short, broad; unguals reduced as in *Camelus*.

The most abundant species in the present collection is *A. procerus*. The material is all fragmentary and it appears better to reserve description until better specimens are at hand.

Cervidæ

Dromomeryx Douglass¹

The affinities of *Dromomeryx* and its allies appear to be closer to the Tertiary Giraffidæ than to the Cervidæ with which they are usually ranked. Pending a revision of the American later Tertiary ruminants I nevertheless retain this group as customarily arranged.

Dromomeryx whitfordi Sinclair

A number of lower jaws and upper teeth, Nos. 17331-17335, are referred to this species, as they agree with Sinclair's paratype. The teeth show considerable variation in size and some variability in pattern, but always the crowns are very low, the surface strongly rugose; the lower molars always show the "*Palæomeryx* fold"; the metaconid of p_4 is expanded anteriorly and posteriorly into a wide plate; the heel of m_3 has its inner cusp opposite the posterior end of the hypoconid crescent.

Cervavus Schlosser²

Schlosser uses this name to designate a stage intermediate between the *Palæomeryx* stage of cervid evolution and the more specialized cervid genera.

I cannot find any very clear generic distinctions from *Amphimoschus* Bourgeois, 1873,³ as described and figured by Mayet, 1908⁴; but this genus is from an older geological horizon.

¹ Ann. Carn. Mus., V, 1909, p. 461.

² 'Fossilien Säugethiere Chinas,' Abh. bay. Akad. Wiss., XXII, 1903, p. 116. Type, *Palaeomeryx Oweni* Koken.

³ Bourgeois. Journal de Zoölogie, II, 1873, p. 65, Pl. x.

⁴ Mayet. 'Mam. Mioc. de l'Orleanais, etc.,' Ann. Univ. Lyon, N. S., Sci., Med., 1908, Fasc. 24, p. 285, Pl. x and text figs.

Cervavus sinclairi, new species

Types: three lower jaws, Nos. 17338, 17337, 17336.

Size of *D. whitfordi* and very like it in construction but distinguished by higher crowned and less rugose molars with no trace of palæomeryx fold, metaconid of p_4 smaller, less extended anteriorly, heel of m_3 with its inner cusp wholly or almost wholly behind the posterior wing of the hypoconid crescent.

In addition to the two species above cited, a larger and a smaller species of *Dromomeryx* and two other species of *Cervavus*, one smaller than *C. sinclairi*, are indicated by single teeth.

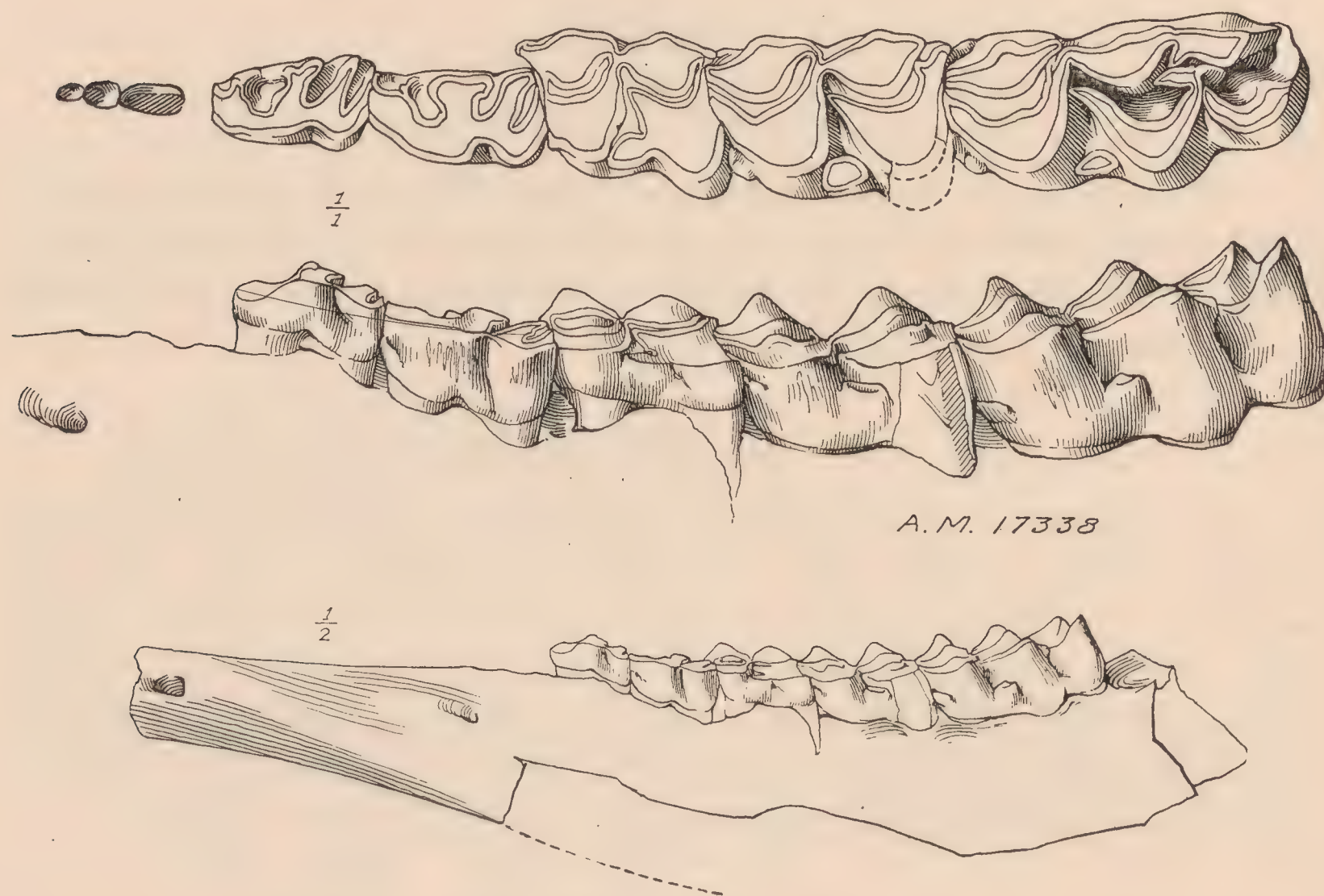


Fig. 17. *Cervavus sinclairi*, new species. Lower jaw, type specimen, half natural size; with crown and external views of teeth, natural size. Snake Creek beds, expedition of 1916.

Blastomeryx elegans Matthew and Cook

This species is represented by a number of jaws which add nothing to the known characters.

The relationships of the above species of "Cervidæ" are not clear. *Dromomeryx* is undoubtedly allied by its teeth to the European *Palæomeryx*; its "horns" are of the giraffid type, distinct from the deciduous antlers of cervids and merycodonts and from the true horns of the Bovidæ.

Cervavus sinclairi and other nearly related species of the Lower Pliocene are close to *Odocoileus* in dentition but, until the character of their antlers is known, it is not safe to refer them to that genus for they equally resemble various other modern cervid genera, especially the South American *Blastocerus* and *Hippocamelus*. *Blastomeryx* is probably a primitive survival but possibly has relations to the Central American brockets.

Antilocapridæ

Merycodus Leidy

The reference of *Merycodus* to the Antilocapridæ is now well warranted. The genera *Sphenophalos* and *Ilingoceras* from the Pliocene of Thousand Creek and skull material of *Capromeryx* from the La Brea beds show intermediate conditions in one way or another. *Merycodus* is very common in the Snake Creek beds, by far the most abundant of the smaller forms. Three species are represented, but only one is well known and this appears to be indistinguishable from *M. necatus* Leidy.

Merycodus necatus Leidy

Two incomplete skulls, Nos. 17339 and 17340, and a large series of upper and lower jaws afford some interesting data concerning this species.

In the first place, comparison of this series with a large series (unpublished) of *M. necatus* jaws from Valentine, Neb., in the University of Nebraska Museum, which I was permitted to examine through the courtesy of Professor Barbour, shows that there are no constant differences of size between the Valentine jaws and the Snake Creek material described in 1908 as *M. necatus sabulonis*. No other valid characters have been detected. The type of *M. necatus* is from Bijou Hills and is in the American Museum but, in absence of topotypes, it affords no good specific characters except size. The Valentine series are topotypes of Leidy's subsequently figured specimens (1869).

One of the skulls from Snake Creek has the molars well worn; in the other, they are comparatively little worn. The teeth are smaller than in *M. osborni*, the premolars more reduced, the molars more hypsodont. A rudimentary third lobe sometimes occurs on m^3 ; also a rudimentary inner pillar. The antlers in both skulls are two-tined; they branch rather high up on the beam, and the tines are rather small. The burr is single on the younger, double and partly triple on the older individual. Four separate

antlers of the same type were found. It appears, therefore, that in this species there were only two tines in the mature individuals, whereas in *M. osborni* there are three, the antlers being much larger.

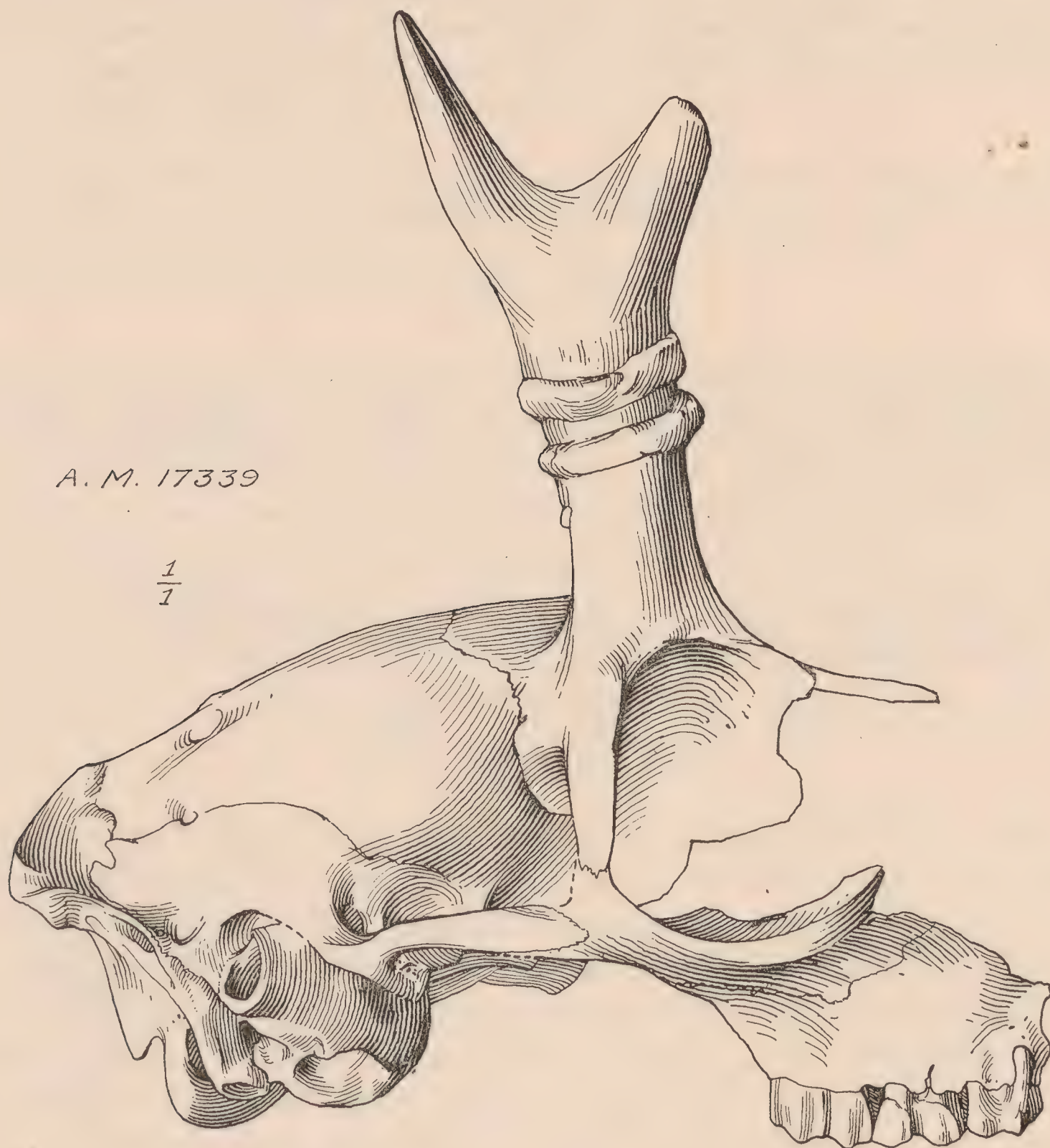


Fig. 18. *Merycodus necatus* Leidy. Incomplete skull; natural size. Note the supra-orbital position of the antlers and the sharp bend of the basifacial upon the basicranial axis. The molar teeth are heavily worn, showing that the skull is of an old individual, but the antler has only two tines. Two complete burrs and traces of a third are preserved, indicating repeated shedding of the antlers, probably annual. Sinclair quarry, Snake Creek beds.

Affinities of Merycodus

Winge¹ regards this genus as a true deer and not related to *Antilocapra* which he places in the Bovidae. Following is a translation of his remarks.

¹ Winge. 1906. Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa etc. E Museo Lundii, III, part 1, p. 221.

A peculiar group of American deer is represented by the Tertiary North American *Merycodus* (syn. *Cosoryx* auct. Cope and Matthew) and its Tertiary North American relatives, the more primitive *Blastomeryx* and the less primitive *Capromeryx*. . . . *Merycodus* is known from the nearly complete skeleton, the others only from small parts. *Merycodus* is a deer with two or more tined horns certainly shed annually, with burr, and in all respects standing close to the other Cervidæ except in the form of the posterior cheek teeth, which are high crowned as in the highest Bovidæ. Matthew sets forth a number of other peculiarities by which it should resemble Bovinæ especially *Dicranoceras* ("Antilocapra") and he makes it the type of a special family Merycodontidæ which he, in spite of the horns [antlers], places beside the Antilocapridæ among *Boöidea typica*, which he has set in opposition to *Boöidea cerviformia*, quite in sympathy with Cope's presentation; yet he admits that nearer affinities with the deer are possible although not probable.

But not a single one of the peculiarities, excepting the height of the cheek teeth, which Matthew sets forth as resemblances to the Bovidæ is, in truth, decisive; not one of them is strange for Cervinæ; on the contrary, *Merycodus* has, in the form of the 3rd and 4th united metacarpals and likewise the metatarsus, a distinct deer peculiarity, the back side of the bone is excavated channel-fashion (according to Matthew's description). There cannot be the least doubt that *Merycodus* is a deer that has acquired high-crowned back teeth like the highest, not the more primitive, Bovidæ; it is not a bovine that has developed deer-antlers. Another question is whether the *Merycodus* group had its origin in the older deer-forms which are known from North America referred to *Palæomeryx* [i. e. from *Dromomeryx*] or from the deer allied to *Cervulus*, or whether it came from the same stem as the *Subulo* group [*Qdvcoileus* and its allies]; hereupon one cannot be certain. The condition of the vomer in *Merycodus* and its relatives, a point which would have weight in this respect, is not shown in the drawings. As against the *Subulo* group, *Merycodus* (but not *Blastomeryx*) differs not alone in the high crowned cheek teeth but in the complete lack of 2nd and 5th metacarpals.

Winge reckons *Antilocapra* among the Bovidæ and therefore does not allow that it has anything to do with *Merycodus*. The channelling of the back of the metapodials, which he regards as a cervid peculiarity, is a primitive character; it is retained in most of the Cervidæ, in *Antilocapra*, and in some primitive true Antelopes, e. g. *Cephalophus*, but it is present in all the Miocene pecora that I have examined, as well as in *Merycodus* and *Blastomeryx*. Its disappearance in most modern Bovidæ is an incident of specialization. The bending down of the basifacial axis is also a specialization and it undoubtedly occurs to a varying extent in some modern Cervidæ; perhaps Winge is right in attaching no great weight to it. The forward position of the antlers I have not seen matched in any Cervidæ, and it does constitute a marked approach to the supra-orbital position of the horns in *Antilocapra*. The peculiar character of these last and the intermediate types in *Capromeryx* and *Ilingoceras*, indicating derivation from a deciduous branching antler, confirm the affinity to *Merycodus* for which the principal weight of evidence is in the teeth. The height and construc-

tion of the molars and the construction of the premolars in *Merycodus*, *Capromeryx*, and *Antilocapra* can hardly be studied in detail without concluding that they are rather nearly related and should be set apart from either Cervidæ or Bovidæ. *Merycodus* and *Capromeryx* retain a distinctly more primitive stage in premolar construction, which might be derived from the *Blastomeryx* type, not from the later *Odocoileus* group, and certainly not from *Dromomeryx* (which is not older than *Merycodus*, as Winge states, but a contemporary).

Without entering into the problem of the exact phyletic relations, it may be said that to disassociate *Merycodus* and *Antilocapra*, throwing the one into the Cervidæ and the other into the Bovidæ as Dr. Winge would arrange them, appears to be a quite untenable arrangement, in spite of his very positive statements; but whether the affinities of the Antilocapridæ, including *Merycodus*, etc., are closer to the deer or the true antelopes is, in my opinion, an open question. The whole matter must be viewed in the light of the relative geological age of the various genera to be considered (a point to which Dr. Winge gives very little attention, here or elsewhere), of their present distribution, and of the centers of dispersal of the ruminant groups. *Merycodus* of the middle Miocene had already acquired complex antlers, hypsodont teeth, and other highly progressive characters which do not appear in the true Cervidæ until later; per contra, its premolar construction is archaic.

Schlosser¹ has attempted to derive *Merycodus* from the Oligocene *Hypisodus*, but, aside from the precocious hypsodontism of this genus, there is nothing to support his view. On the contrary, the first lower premolar of *Hypisodus*, as Cope observed in 1874, has become incisiform, as well as the canine, so that there are ten incisiform teeth in the lower jaw; and the outer crescents of the upper molars are of quite different construction from any of the true pecora. Either of these features would serve to exclude it from the ancestry of *Merycodus*. The premolars are also much more reduced, aside from their simple hypertragulid pattern.

? Bovidæ

Whether the genera provisionally referred here are really more nearly related to the antelopes than to the giraffes may well be doubted.

Neotragocerus improvisus Matthew and Cook

The type of this genus and species is a short straight horn-core, showing, especially towards the tip, the soft coarsely cancellous structure of the

¹ See Zittel's 'Grundzüge der Palaeontologie,' Revised Edition, 1911, p. 496.

bovid type of horn-core. The upper molars, provisionally referred to it, may not belong to this genus, but they are nearer to the antelope type than to any other. The lower jaw, provisionally referred by Dr. Sinclair¹ to this form, appears to me more probably a camel, perhaps *Protolabis*, p_4 being too narrow for a bovid or cervid.

Cranioceras unicornis, new genus and species

Type: Amer. Mus. No. 17343, fragment of back of skull with base of horn from Snake Creek beds (Lower Pliocene) of Sioux Co., Neb., Amer. Mus. Exped. 1916.

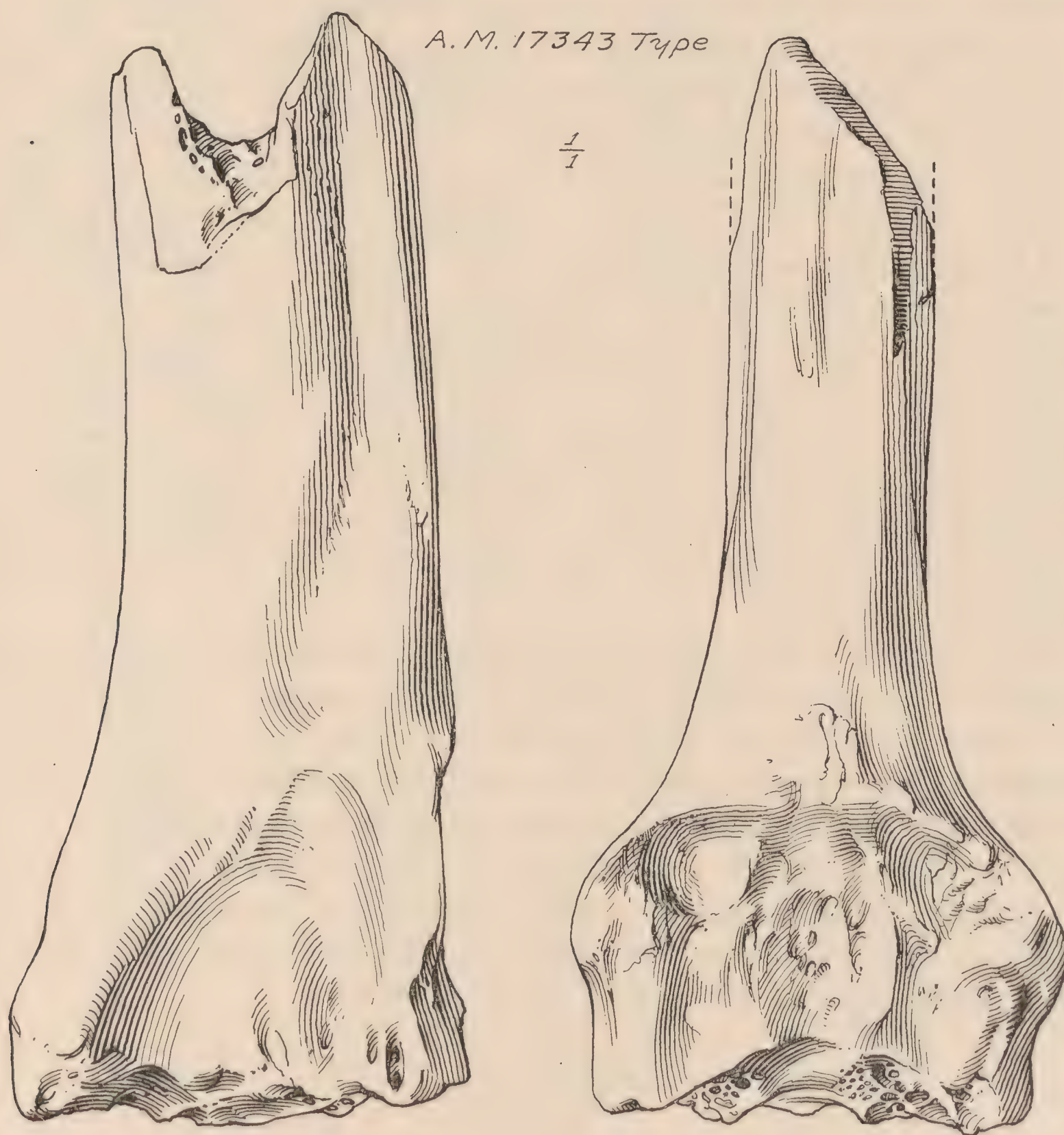


Fig. 19. *Cranioceras unicornis*, new genus, new species. Type specimen; part of occipital horn with adjoining portions of skull. Left side and posterior views; natural size. Snake Creek beds, expedition of 1916.

¹ Sinclair, 1915, *loc. cit.*, p. 93, fig. 16.

A median horn upon the posterior part of the parietal, long, slender, laterally compressed, projecting upward in line with occiput, but with a slight forward curvature.

This is a very extraordinary type of animal. Unfortunately, the type is very incomplete. It is about as large as the larger antelopes, but the median horn, situate on the parietal and projecting upward above the occiput, is wholly different from any described mammal, living or extinct. I suppose it to be more probably an antelope than anything else, but it might be cervid, dicotylid or even perissodactyl. The specific name is based upon the suggestion made by a number of friends — not of course seriously — that it represents the legendary unicorn.

Assuming its ruminant affinities, it is to be noted that five very distinct types of horned ruminants are known from the Snake Creek beds, only two of which, *Merycodus* and *Dromomeryx*, can be correlated with the dentition. The other three are *Cranioceras*, *Neotragoceras* Matthew and Cook, and *Drepanomeryx* Sinclair. Two types of “antelope” dentitions, with moderately long crowned molars, somewhat rugose enamel, one with premolars much reduced, the other with premolars little reduced, have been distinguished. These may correspond to two out of the three horn-types, *Neotragoceras*, *Cranioceras*, and *Drepanomeryx*. The third is perhaps a palæomerycine with short crowned molars like *Dromomeryx* — there are at least two types of ‘palæomerycine’ dentitions distinct from *Dromomeryx* — but, until the discovery of skulls of these various ruminant genera serves to correlate definitely their teeth and horns, it will be impossible to determine their association.

I have referred tentatively to this animal a remarkable lower jaw, No. 17344, indicated as a bovid by the breadth and pattern of the premolars, the moderate height and width and smooth surface of the molar crowns, and the character of the heel of m_3 , as well as by the form of the front of the jaw and arrangement of the front teeth and entire lack of caniniform teeth. It is distinguished by the great reduction of the premolars. I can find no near relative or parallel among existing Bovidae or the known extinct forms, and the aberrant character of the jaw may well have been correlated with the aberrant skull characters of the type of *Cranioceras*.

REPTILIA

Alligator sp.

A right dentary, lacking the teeth, shows the presence of this genus, not previously recorded from the Tertiary so far as I can discover.

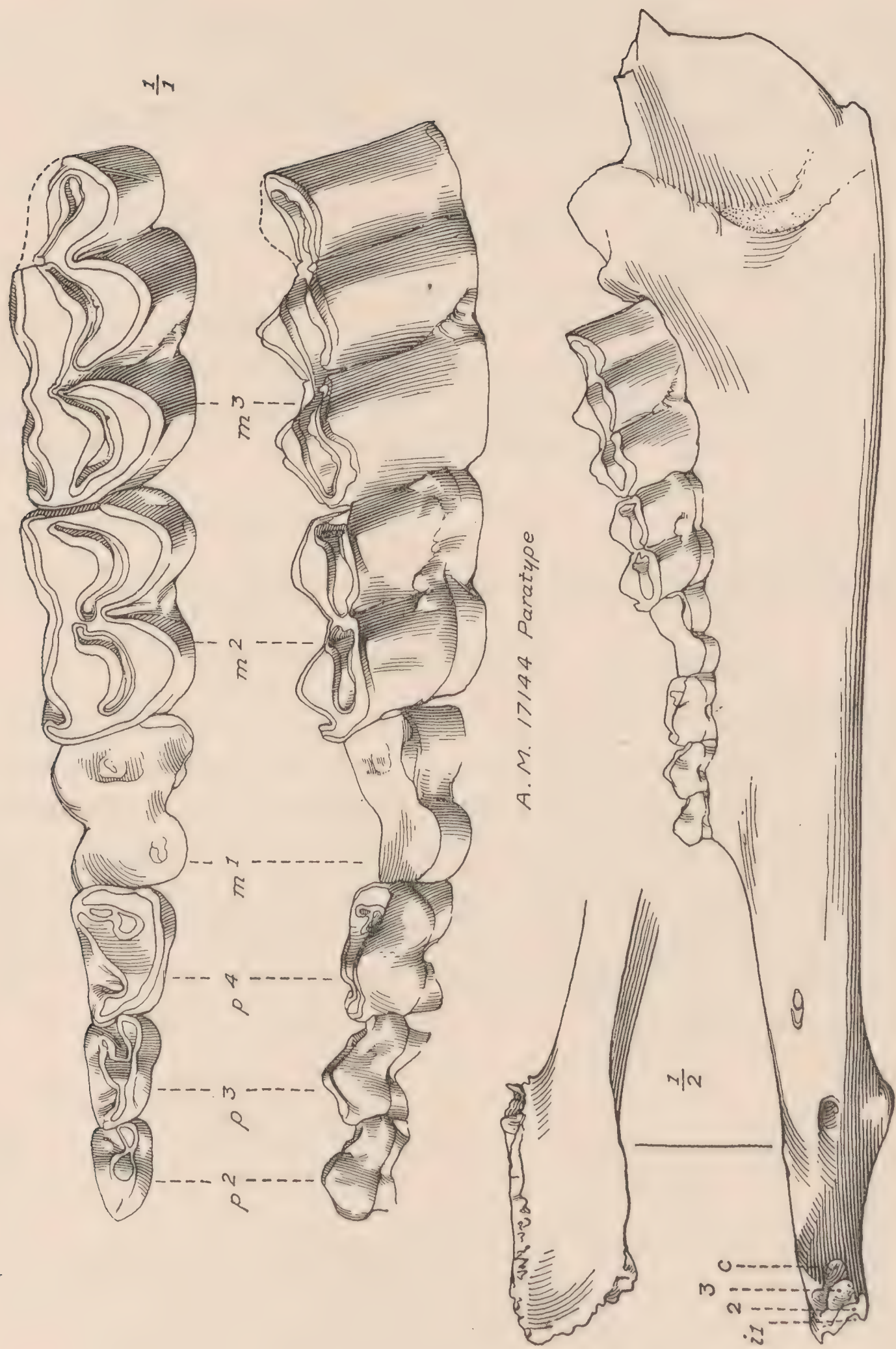


Fig. 20. *Cranioceras unicornis*. Lower jaw provisionally referred to this genus and species; above, crown and external views of cheek teeth, natural size; below, external view of symphysis, one-half natural size. Amer. Mus. No. 17144, Snake Creek beds, expedition of 1916.

AMPHIBIA

Plicagnathus matthewi Cook

A large amphibian nearly related to the giant salamander of Japan and to the American *Cryptobranchus* has been recently described by Mr. Harold J. Cook from part of a lower jaw found by him in the Snake Creek beds.

PISCES

? *Ameiurus* sp.

A lower jaw and other fragments of a large catfish are identified by Mr. J. T. Nichols as probably *Ameiurus*, agreeing in size with *A. lacustris*, whose present range is from the Saskatchewan and the Great Lakes in the north to Texas in the south.

NOTES UPON THE PLEISTOCENE OF WESTERN NEBRASKA

SHERIDAN AND LOUP RIVER BEDS

The older Pleistocene "Equus beds" are widely spread in western Nebraska, and are readily recognized by the bones of *Equus* which are the most abundant fossils in them. In western Nebraska the most productive locality is the "Hay Springs quarry," south of the Niobrara River in Sheridan Co. In 1902 I published a list of this fauna¹; since then the Equidæ have been revised by Dr. O. P. Hay, and some changes in nomenclature or identification now appear advisable in other groups. A few additions have been made.

Canidæ*Canis* cf. *occidentalis*

jaw fragments, etc.

" " *latrans* Say

jaws, etc.

Ursidæ*Arctotherium* sp.

astragalus; metacarpal

Felidæ*Smilodon nebrascensis*, new species

lower jaw

Felidæ div. indet.

limb and foot bones

¹ Pleistocene Fauna from Hay Springs, Nebraska. Bull. Amer. Mus. Nat. Hist., XVI, 1902, pp. 317-322.

Sciuridæ*Cynomys* cf. *ludovicianus*

palate

Muridæ*Fiber nebracensis* Hollister

skull; jaws

Microtus sp.

jaws

Castoridæ*Castoroides* sp.

teeth, humerus, astragalus

Geomyidæ*Thomomys* sp.

jaws and fragments

Megalonychidæ*Myiodon nebrascensis* (Brown) ? = *M. harlani*

skull, jaws, parts of skeleton

Megalonyx sp. (*vide infra*)

foot bones

Equidæ*Equus niobrarensis* Hayskull, numerous jaws, and all
parts of skeleton“ *excelsus* Leidy

jaws, ? foot bones, etc.

Elephantidæ*Elephas columbi* Falconer

skull; tusks, teeth, etc.

Dicotylidæ*Platygonus*

palate, parts of jaws, etc.

Camelidæ*Camelops kansanus* Leidyjaw fragments and bones of
skeleton“ cf. *vitakerianus* Cope

jaws, etc.

“ *americanus* (Wortman)

lower jaw

Antilocapridæ*Antilocapra* cf. *americana* Ord

teeth, foot bones, etc.

Capromeryx furcifer Matthew

lower jaw

The identity of this fauna with the Aftonian interglacial fauna of Iowa has been fully demonstrated by Calvin¹ and confirmed by Hay.²

The “original Loup River” formation, described by Hayden in 1858 and from which Leidy described the species *Elephas imperator*, *Equus excelsus* and ?*Hipparion* sp., appears to have been the beds exposed along

¹ Calvin, 1909. Bull. Geol. Soc. Amer., XX, pp. 341-356, Pl. xvi-xxvii.

² Hay, 1914. Iowa Geol. Sur. Ann. Rep. for 1912, XXIII.

the Middle Loup west of Seneca, underlying the sandhill deposits and distinguished by a more earthy consistency, pale yellowish gray color with a slightly greenish tinge, and slightly consolidated, in distinction from the yellower and completely unconsolidated sandhill material.

A small fauna was secured from these beds in 1916, as follows.

<i>Equus</i> sp., cf. <i>niobrarensis</i>	teeth and foot bones
Camelid cf. <i>Camelops</i> , 2 species	foot bones
<i>Platygonus</i> , 2 species	jaw fragments
Megalonychid indet.	part of scapula
<i>Thomomys</i> sp.	several lower jaws
<i>Cynomys</i> sp.	lower jaw
<i>Scalops</i> sp.	"
<i>Lutra</i>	jaw fragments, no teeth

No proboscidean bones were observed.

The westward route of Hayden's party as shown on Leidy's map in the 'Extinct Mammalian Fauna of Dakota and Nebraska,' 1869 (Lieut. Warren's Exped.), was up the Middle Fork of the Loup River, but side trips appear to have been made to the Dismal and North Loup River. The whole region is sandhill country with very few exposures and these only along the river valleys. On the Middle Loup, the only exposures found were these beds west of Seneca; on the Dismal, a little Tertiary (Pliocene) is exposed in places underlying similar Aftonian beds; and possibly it was from these that the *Hipparion* was obtained. But, it appears evident that the typical Loup River horizon, long confused with the Tertiary exposures along the Niobrara (from which came most of the fauna which Leidy and Hayden referred to the formation), is in fact identical with the Sheridan or *Equus* beds of Nebraska and of early Pleistocene age. Osborn, in 1909, showed that it was distinct from the great series of later Tertiary faunas that had been referred to it by Leidy, Cope, and others, but retained it provisionally as a possible late Pliocene horizon. It is now clear that it is early Pleistocene and correlates with the Sheridan and Aftonian. The name has been so generally misapplied that it seems better to avoid using it in any typical sense and to retain it only for the local deposits.

Smilodon nebrascensis, new species

Type: No. 17351, lower jaw from the Hay Springs quarry, Sheridan Co., Nebraska.

The postcanine diastema is decidedly shorter than *S. californicus* jaws with which I have compared it, the cheek teeth about the same size, canine and incisors more

robust. The specimen is not comparable with *S. floridanus* (type a skull with alveoli of upper teeth) although it accords in size. It is incommensurable save as to size with *S. fatalis* of Texas. *Dinobastis* and *Smilodontopsis* appear to be more specialized types of dentition, the cheek teeth more compressed and extended. *Machærodus?* *merceri* and *gracilis* and all other species of *Machærodus* are separated by the presence of p_3 , deeper flange, etc.

I cite this as a new species but much doubt whether it is more than a geographic variant of the *californicus-floridanus-fatalis* group. Its interest is in its occurrence in the typical Hay Springs Pleistocene, correlated with the Aftonian of Iowa, and representing the Lower Pleistocene fauna of the Plains. True cats have been known but sabre-tooth tigers have not hitherto been recorded from this fauna.

? *Arctotherium* sp.

A very large ursid, provisionally referred to this genus, is represented by an astragalus from Box Butte Creek, near the Niobrara River.

Megalonyx, cf. *leidyi* Lindahl

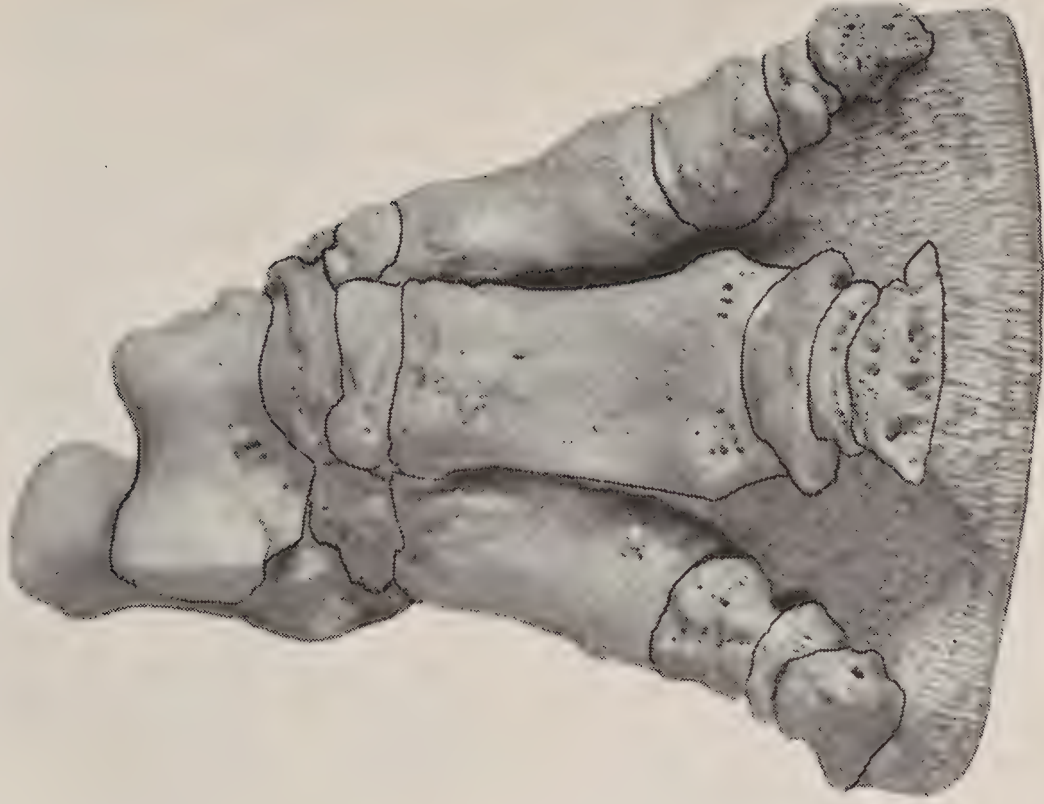
Two or three skeleton bones of *Megalonyx* are identifiable, of which the most characteristic is a metatarsal III, No. 17352 from the mouth of Box Butte Creek. It accords in size with *M. jeffersoni* but is referred to Lindahl's species on ground of geographic propinquity. The genus has been recorded from western Kansas and from eastern Nebraska, not hitherto from the northwestern part of the state.



A. M. 5293



A. M. 9745



Left hind feet of *Aphelops* and *Teleoceras*. No. 8293, *A. megalodus* Cope, Pawnee Creek beds, late Miocene, of Colorado; No. 9745, *A. ceratohinus*, Madison Valley beds, Lower Pliocene, of Montana; No. 2650, Republican River beds, Lower Pliocene, composite specimen from the Long Island quarry, Phillips Co., Kansas. All topotypes.



Fore feet of *Aphelops* and *Teleoceras*. No. 9745, *A. ceratorhinus*, Madison Valley beds of Montana; No. 2650, Republican River beds, composite from Long Island quarry, Phillips Co., Kansas. Both topotype specimens and of Lower Pliocene age.

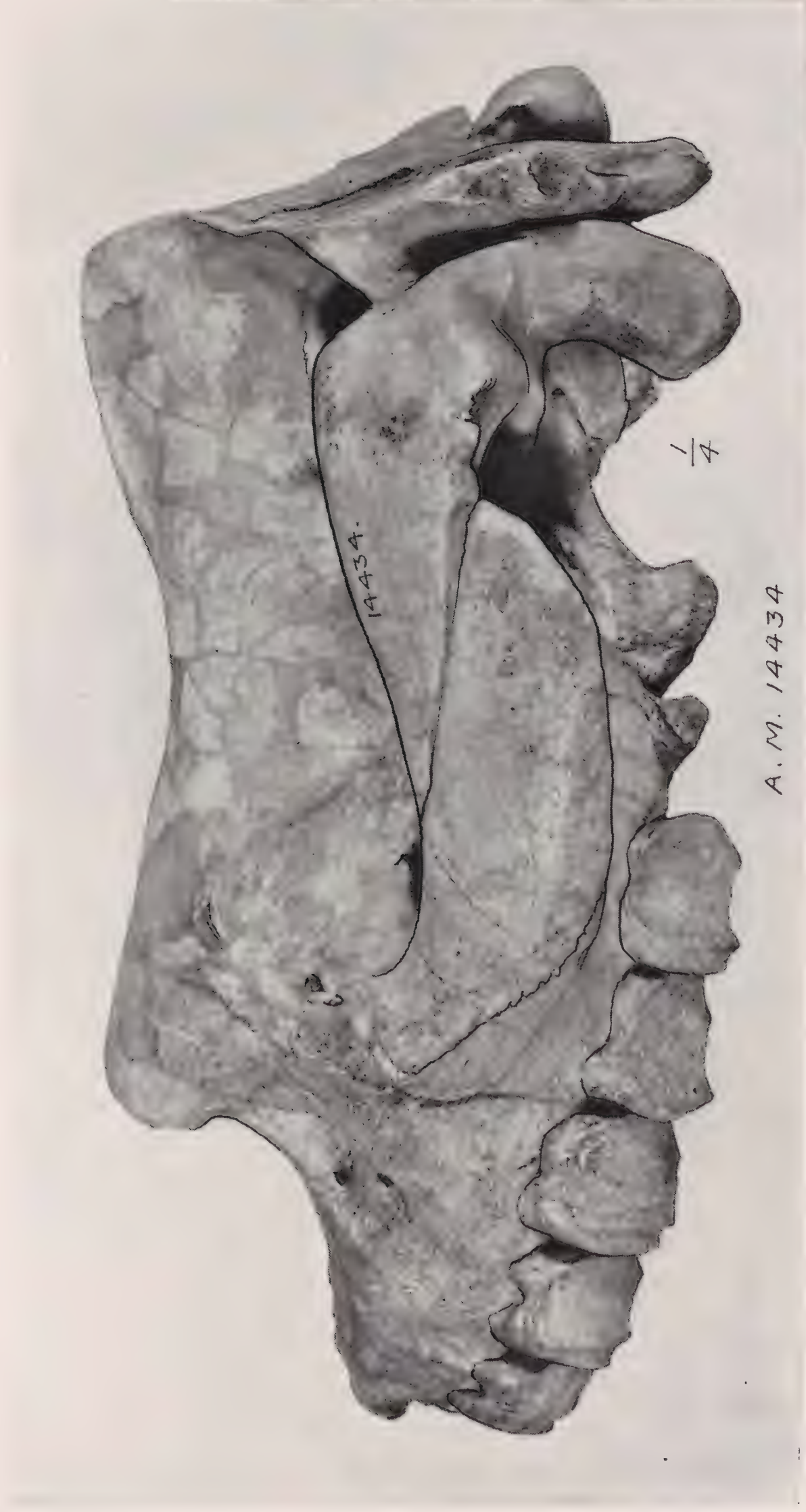


Peraceras troxelli, new species; type skull, palatal view.



A. M. 14434

Peraceras troxelli, new species; type skull, top view.

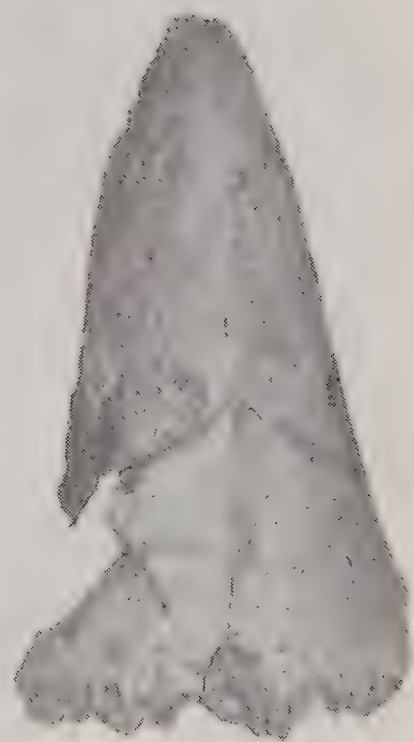


Peraceras troxelli, new species; type skull, side.



Peraceras troxelli, new species; type skull, occipital view. Lower Pliocene, Springview, Keyapaha Co., Nebraska.

A. M. 8293

 $\frac{1}{4}$ 

A. M. 8293 a

Aphelops megalodus, No. 8293, top view of skull; and *Teleoceras medicornutus*, nasals. Pawnee Creek beds, late Miocene, N. E. Colorado. Cope Collection. Both topotypes. The *Teleoceras* is part of a specimen referred by Cope to '*Rhinoceros crassus* Leidy.'

**Article VIII. — MEMORANDA UPON THE ANATOMY OF THE
RESPIRATORY TRACT, FOREGUT, AND THORACIC
VISCERA OF A FŒTAL *KOGIA BREVICEPS***

BY JOHN D. KERNAN, JR., AND H. VON W. SCHULTE

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INTRODUCTION

The present paper forms a continuation of the report¹ upon the structure of the foetal *Kogia* [Physeteridæ; Odontoceti] in the collection of the American Museum of Natural History. The specimen was removed by Mr. Roy C. Andrew from a large female which was stranded at Long Beach, Long Island, and was preserved in alcohol. It measures 109.7 cm. in length. Its external characters, myology, and peripheral nerves have been described previously.¹ In taking up the visceral structures above the diaphragm, our task has been greatly lightened by the labors of Benham² and of le Danois,³ who have preceded us in the study of the soft parts of this

¹ Schulte, H. von W., and Smith, M. deF., 1918, Bull. Amer. Mus. Nat. Hist., XXXVIII.

² Benham, W. B., 1901, On the larynx of certain whales (*Cogia*, *Balænoptera* and *Ziphius*), Proc. Zool. Soc. London, I, p. 278. On the Anatomy of *Cogia breviceps*, Idem, 1901, II, p. 107.

³ Le Danois, E., 1910, Recherches sur l'anatomie de la Tête de *Kogia breviceps* (Blainv.), Arch. de Zool. Exp. et Gen., (5), VI, p. 149. Recherches sur les viscères et la squelette de *Kogia breviceps* (Blainv.) avec un résumé de l'histoire de ce Cétacé, Idem, 1911, p. 465.

interesting whale. As both investigators worked under the difficulties of more or less dismembered material, imperfectly preserved, it has seemed worth while to review briefly the results already attained in the light of our material, while concerning ourselves mainly with topics which, for the reasons stated, these excellent observers were obliged to pass by. In the following report, one of us (Kernan) has charged himself with the examination of the upper respiratory tract and ear, while the other assumes responsibility for the thoracic viscera; other topics touched upon have been worked out in collaboration.

NASAL PASSAGES

The nasal passages of *Kogia* have been described by Benham and by le Danois, both of whom had full grown specimens at their disposal. Their accounts differ one from the other in a number of points, and the material at our disposal appears to present still other variations. To account for these discrepancies, it must be remembered that both the above authors secured their material some days after the death of the animal and after it had been considerably cut up by the neighbors. Thus Benham was able to make no mention at all of the spermaceti organ, which is so intimately connected with the nasal passages. The fact, moreover, that the air passages now to be described are those of a very immature animal undoubtedly accounts for many more of the unlike details.

All accounts agree as to the blow-hole. Its distance from the tip of the snout naturally varies with the size of the animal. It is here situated 10.5 cm. caudad from the rostral extremity, largely to the left of the midline, crescentic in form, with the concavity of the crescent dextro-caudad. It is bordered by two thick lips made up of dense white fibrous tissue covered by smooth, black epithelium. The rostral lip overlies the caudal in a manner to provide for closure by water pressure. The muscles controlling the movements of the blow-hole have been described elsewhere.¹ A distinct sphincter was not found here, such as was described by le Danois, though the appearance of the tissue on cross-section suggests the presence of encircling muscle bundles.

In addition to its dorsal fold, which is thin and overlies the caudal lip, the rostral has also a ventral fold which juts under that structure. Thus, on cross-section, it is semilunar in shape and holds in its concavity the caudal lip, which on its part is convex.

This ventral ridge of the rostral lip of the blow-hole merits further

¹ Schulte, H. von W., and Smith, M. deF., 1918, Bull. Amer. Mus. Nat. Hist., XXXVIII.

description. At the dextral limit of the orifice it is sharp, prominent, and presents on its very edge a transverse slit, which is the opening into the right nasal passage. As it passes sinistrad it assumes a rounded contour and turns ventrad till, finally vertical in direction, it forms on the rostral wall of the left nasal passage a rounded eminence which gives a crescentic cross-section to that canal. This is doubtless the prominence which both Benham and le Danois described as forming the floor of the vestibule.

The blow-hole opens into a canal 2 cm. long, designated as the vestibule. It is merely the space between the lips, has no floor, and passes directly into the left narial passage. The line of demarcation between the two can be drawn at the ventral margin of the rostral lip, the left nostril being the space between this and the groove below the caudal lip into which it fits. The right nostril is the small slit in the edge of the fold near its dextral extremity.

Both Benham and le Danois described the vestibule as having a floor; of this there is here no trace. According to Benham, this floor is formed by a protrusion of the rostral lip which juts caudad near its dextral extremity. This turns sinistrad, rendering the left narial passage crescentic, and is continued in the mesal wall of that passage to the naso-pharynx. Le Danois describes the same protrusion in the floor of the vestibule and ascribes it to the presence of the head of the caudal spermaceti chamber.

In the animal here under description, the ventral fold of the anterior lip, doubtless identical with that portrayed by Benham, takes a vertical position in the rostral wall of the left air passage. It may be that growth converts the above described fold into the prominence pictured by Benham, and then the vestibule would indeed have a floor. That this floor is due to the presence of the spermaceti organ does not seem probable from the evidence at hand, for, as we shall see later, the caudal spermaceti chamber turns its pole in the opposite direction.

Benham placed the right nostril in the caudal lip of the blow-hole, exactly opposite to where we find it. This discrepancy may be explained by a shifting of the opening due to age and growth. Le Danois placed the right nostril in the floor of the vestibule, and from his figure we gather that it penetrated the mass which, according to Benham, formed the floor. If it is correct to conceive of the ventral margin of the rostral lip of the blow-hole eventually developing into the floor as described by Benham, then we should expect to find the right nostril just where le Danois put it.

Ventral to the vestibule is a large space, 1 cm. in dorso-ventral extent, the caudal wall of which is so lax as to lie in parallel folds. These take their origin in the extreme dextral angle of the canal and run sinistro-ventrad. Evidently this short portion of the canal is distensible. Close examination of the wall here shows it to have faintly trabecular structure.

In the sinistral angle of the blow-hole sac are a number of small openings which lead into finger-like pouches. These are placed in three layers. The most dorsal of these consists of a single pouch which has its orifice in the rostral lip. The second layer of several pouches has a single large opening, a slit .5 cm. in extent in the caudal lip opposite the first. The third layer,

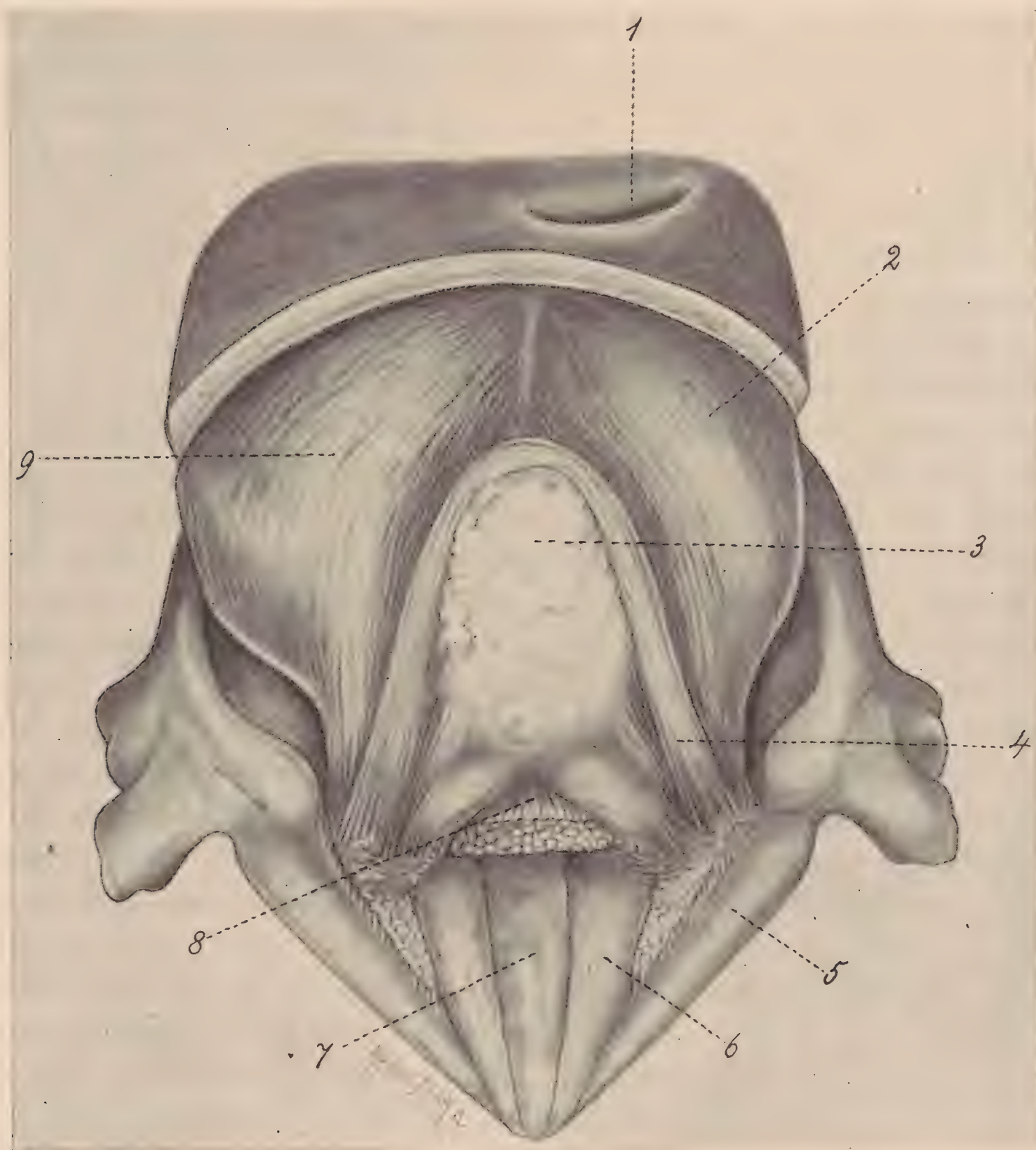


Fig. 1.—Exposure of muscle of spiracular sacs, rostral view.

1. Blow-hole.
2. Pouch from dorsal spiracular sac covered by muscular sheath.
3. Head of caudal spermaceti chamber.
4. Mass of muscle bundles about tip of spiracular pouch.
5. Maxilla.
6. Premaxilla.
7. Meso-rostral cartilage.
8. Longitudinal muscle bundles from rostral walls of air passages.
9. Roof of dorsal spiracular sac sheathed by fibro-muscular layer.

most numerous, takes origin by several mouths from the distensible space below the caudal lip.

The whole conglomeration of tab-like pouches forms a mass 2.5 cm. in

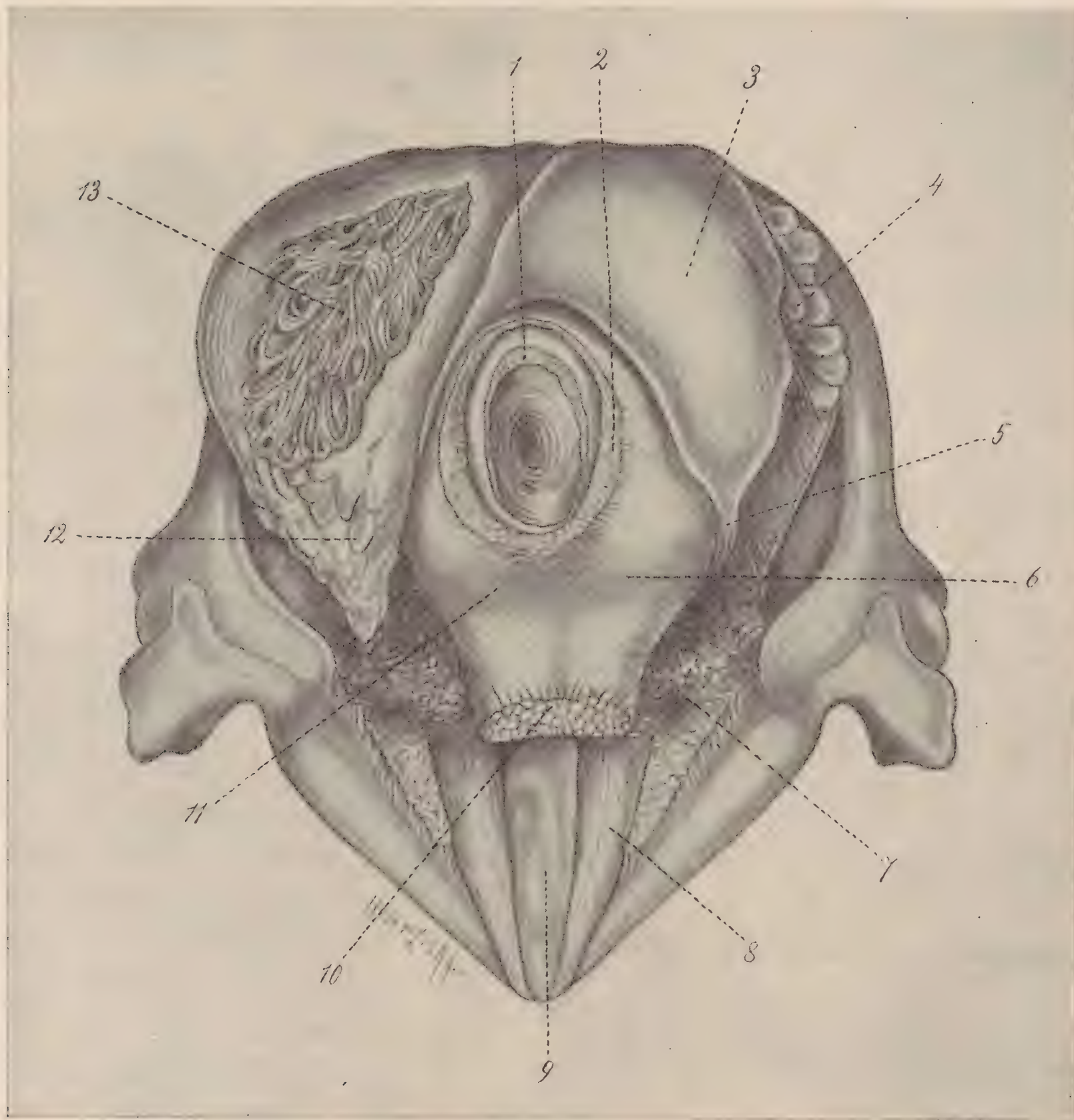


Fig. 2.— Exposure of spiracular sacs and spermaceti organ, rostral view.

1. Cut edge of spermaceti organ.
2. Cut edge of "case."
3. Spiracular pouch, extension to left of dorsal spiracular sac.
4. Spiracular pouch from left air passage.
5. Tip of spiracular pouch bound down by muscle.
6. Rostral wall of left air passage.
7. Cut edges of muscular sheath overlying air passages and spermaceti organ.
8. Premaxilla.
9. Meso-rostral cartilage.
10. Cross section of longitudinal bundles from rostral walls of air passages.
11. Rostral wall of right air passage.
12. Spiracular pouches from dorsal spiracular pouch.
13. Exposure of trabeculated roof of dorsal spiracular sac.

length extending sinistro-caudad from the wall of the air passage. These pouches are closely bound together by fibrous tissue, and the mass is interlarded with muscular fibres.

The trabeculation and pouching of this portion of the left narial passage should be particularly noted, as they are repeated on the right side in a greatly exaggerated manner. They were not noted by Benham and le Danois.

From this area of trabeculation and pouching the canal passes ventrad, gradually narrowing till it reaches the opening in the bone. The convexity of the rostral wall increases in extent till the cross-section of the passage is nearly semicircular. The convexity is not continued through the bony portion of the passage into the naso-pharynx, as Benham found it, but terminates at the level of the bone with a free extremity, which serves as a plug to block the nasal passage and prevent the ingress of water.

As to structure, the convexity in the rostral wall of the left air duct is the relief of a mass of muscular fibres which take origin in the fibrous sheath of the wall and pass mesad and rostrad to insert mainly in a raphe which separates these fibres from similar ones of the right air passage. The more ventral fibres reach far forward on the midline of the rostrum. The more dorsal fibres arch about the caudal spermaceti chamber and insert in the fatty areolar tissue which forms the mass of the snout.

The function of this muscle is, apparently, the opening of the canal to permit the free passage of air.

As has been said, the right nostril is a slit, .75 cm. long, in the margin of the rostral lip of the vestibule near its dextral extremity. From this opening a short canal passes dextrad and opens into a large cavity, the so-called superior respiratory sac (Benham). From the rostral wall of the canal a number of large openings lead into a purse-like structure which extends ventrad and completely overlies the left narial passage. The interior of this structure is divided into numerous communicating cavities by anastomosing bands passing from wall to wall. These spaces are lined by smooth membrane. The walls are fibrous. The whole structure is overlain by a sheet of fibro-muscular tissue which is attached dorsally about the blow-hole and ventrally to the maxilla. The muscular tissue concentrates about the tip of the structure and there forms a distinct band which firmly anchors it to the maxilla. This extension of tubules from the right narial passage toward the left is correctly described by Benham and figured in a diagram given by him. It is not mentioned by le Danois.

The so-called superior respiratory sac is a large oval expansion of the right nasal passage, measuring 3.5 by 5 cm., the long measurement passing dorso-ventrad, the short caudo-rostrad. In a general way, the cavity

faces dextrad. It may be described as having a floor and a roof, which meet at an acute angle at every point of the circumference.

The floor is markedly convex, rising to a sharp eminence in its center.¹ The apex of this shows a thin-lipped, transverse slit, 1.8 cm. in length; the aperture leads into the continuation of the passage.

The roof of the cavity, 1 cm. thick, is composed of a mass of anastomosing trabeculæ. The spaces between the trabeculæ communicate freely with one another and with the main cavity. So the ental surface of the roof is exceedingly irregular. This surface and the intertrabecular spaces are lined by a continuous, smooth, dark membrane.

From the junction of the floor and the roof, for the whole of the circumference except directly rostrad, spring numerous glove-like pouches, such as were found on the left side. Along the caudal border, they are so long as to be folded back on themselves and the closed extremities of these point dorsad. Elsewhere, they point ventrad. The whole mass is overlain by fibro-muscular tissue, the muscular fibres of which concentrate about the circumference where they form a distinct sheet and firmly bind the whole to the maxilla.

Both Benham and le Danois, in their text and cuts, gave fairly adequate descriptions of the right respiratory sac, its trabeculated wall, and the surrounding pouches. If we compare conditions here with those found on the left side, we will see that it represents a great development of identical structures. There, too, is found a distensible cavity with trabeculated walls, from whose margins spring a fringe of pouches forming a mass covered by fibro-muscular tissue and interlarded with muscular fibres. So we may say that equivalent structures are found on the two sides, though greatly reduced on the left.

Benham raised the question as to where the true right nostril lies: at the opening into the vestibule, or in the floor of the respiratory sac. On account of the change in the color of the epithelium in the respiratory sac, he decided in favor of the former location. If we consider the condition found in *Kogia* a development from that found in such forms as *Tursiops*, where there is a single, large, dilatable pouch from which open two equal-sized air passages, guarded by valves, we may decide that the division of the right and left pouches is only a secondary separation of what was originally one cavity and that the true right nostril lies in the floor of the respiratory sac. On the other hand, if we hold that the condition found in *Balænoptera* — two nostrils, each with a "spritz-sac" — is the primitive one and that *Kogia* is merely a midway stage toward the complete fusion of

¹ *Musseau du singe* of Pouchet and Beauregard.

Tursiops, then we should be justified in putting the right nostril at the termination of the right air passage in the vestibule. Since *Kogia*, as far as its nasal passages are concerned, is much more highly specialized than *Tursiops*, the first interpretation, placing the nostril in the floor of the respiratory sac, appears more probable. However, such a question could only be surely decided upon a basis of much more material than is at our disposal.

In the matter of the function of the respiratory sac and the pouches connected therewith, we are as much in the dark as in that of anatomical interpretations. That they are widely distensible, we know from their structure; and that they actually are widely distended in respiration, Andrews has demonstrated, at least for baleen whales. On the other hand, we may surmise from the arrangement of the muscles around them that they are powerfully compressed at times. Their large development and copious blood supply argue an active function. This must have something to do with the preparation of the inspired air for respiration, though, after all, it can effect only a small portion of it since the larger percentage goes directly to the lungs through the more direct left nasal passage.

The object of the powerful compressor muscles is doubtless to insure against the entrance of water when the animal dives.

The continuation of the right nasal passage begins at the prominent papilla, above described, in the floor of the respiratory sac. At this point it is as wide as the slit, that is 1.8 cm., with flat walls rostrad and caudad which are in close contact. It narrows as it passes ventrad and, at its entrance into the bony passage, is only 0.4 cm. wide. On reaching the surface of the rostrum, it turns sinistrad a little, then caudad as it enters the bone and proceeds to the naso-pharynx. It nowhere has any connection with the so-called second respiratory sac. Its walls are composed of a mass of fibro-muscular tissue, the fibres of which lie in the horizontal plane and turn inward to insert in the median raphe, which also receives the fibres from the left side. This would indicate that this nasal passage is capable of distension like the left, though much less so as the muscular wall is much thinner. A probe can be passed on into the naso-pharynx.

This condition of the right air passage is entirely different from that found by Benham and le Danois. Both of these authors state that the air passage, on leaving the first respiratory sac, enters directly into the second. In this specimen, we find the connection with the second or lower respiratory sac just at the point where the nasal passage turns sinistrad before entering the bony canal. In this portion of its course it loses its caudal wall, the gap being the opening into the sac. Thus this structure is a caudal protrusion from the air passage.

The ventral spiracular sac is so intimately connected with the organ of spermaceti that it seems best to describe that structure first. Its rostral extremity lies in an arch formed by the two nasal passages as they

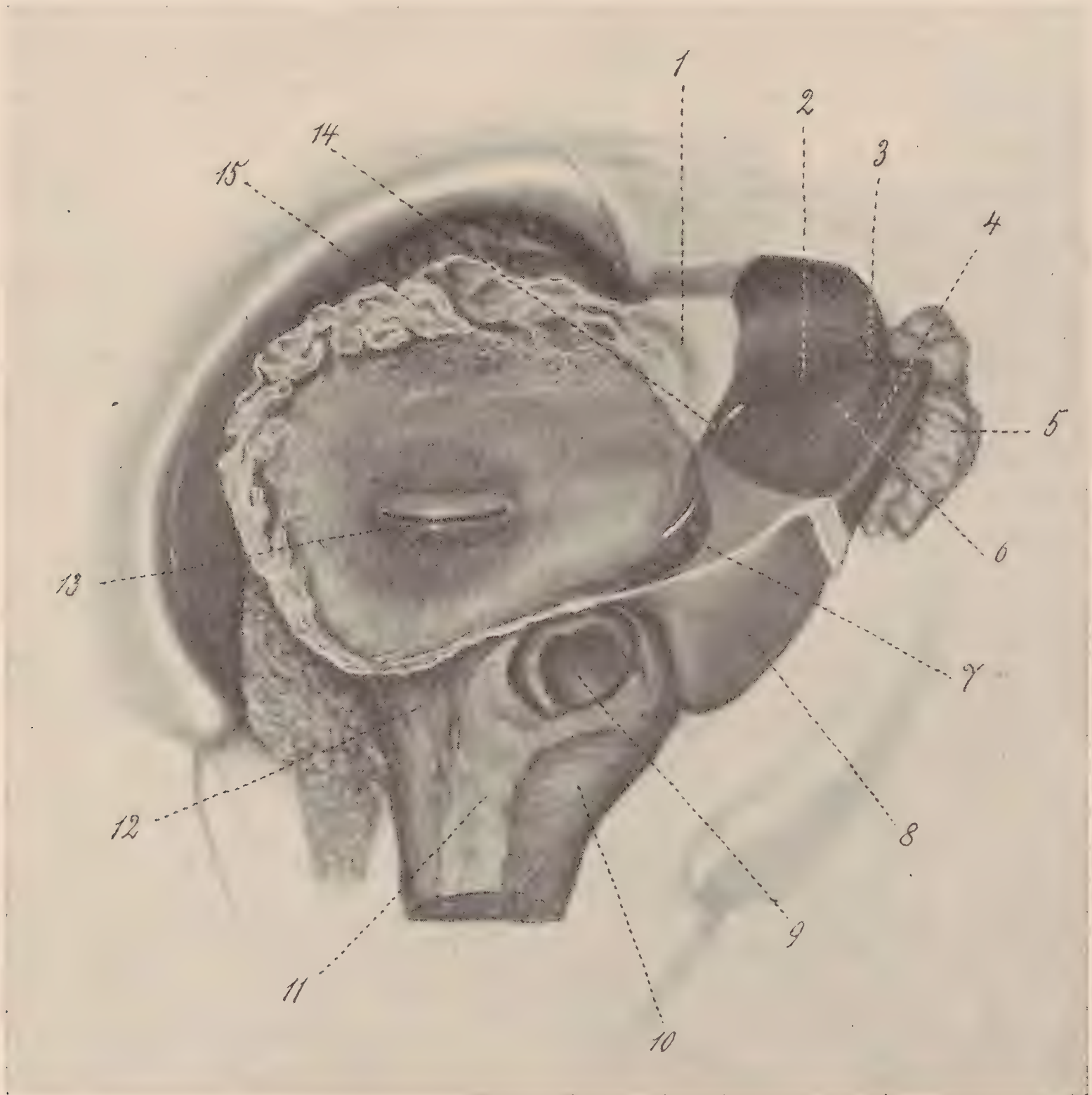


Fig. 3.— Exposure of floor of dorsal spiracular sac and vestibule.

1. Cross section of caudal lip of blow-hole.
2. Orifice of left nasal passage.
3. Openings into spiracular pouches.
4. Mass of spiracular pouches, left side.
5. Rostral lip of blow-hole, ventral fold.
6. Orifices of "spiracular pouch" extending to left.
7. "Spiracular pouch," extension to left from spiracular sac.
8. Spermaceti chamber.
9. Wall of "case."
10. Median raphe.
11. Rostral wall, right air passage.
12. Orifice of right air passage.
13. Probe passed through canal from vestibule to dorsal spiracular chamber.
14. Cut edge of roof of dorsal spiracular sac.

ascend from the surface of the rostrum to the blow-hole. The wall of each is composed of fibro-muscular tissue, the fibres of which converge below into a median raphe. More dorsal bundles pass rostrad and lose themselves in the great mass of fatty areolar tissue which forms the bulk of the snout. On the removal of this tissue, the cut edges of the fibres which meet above, rostrad to the blow-hole, form an arch which frames the spermaceti organ. So this lies in a case, the walls of which are composed of fibro-muscular tissue. The organ itself has a fibrous wall of greatly varying thickness and contains a sponge-like network of delicate fibres. The interstitial spaces, which are largest at the rostral extremity, are filled with fluid. The tissue is not in condition to make a histological examination of value. Le Danois and also Pouchet and Beauregard have covered this matter rather thoroughly. The illustration of le Danois of the sagittal cut of the head gives a very good idea of the box-like character of the space in which the spermaceti organ lies. No distinct wall covering the rostral extremity of the spermaceti organ could be made out. The tissue seemed to change quite suddenly from the rather dense fatty areolar tissue, which forms the bulk of the snout, to the delicate sponge-like structure of the spermaceti organ. Le Danois found the spermaceti chambers completely encased by a fibrous wall. This lack of a complete enclosure, rostrally, of the spermaceti chamber may be taken, with the non-development of the anterior spermaceti chamber, as another evidence of immaturity.

From its rostral extremity, where it has its greatest diameter, the organ, which is a tube-like structure, passes caudad, then curls dextrad behind the right nasal passage. Its general shape is like that of a crooked finger. Its termination, which is again directed rostrad, turns upward at its very tip. This elevation of the tip gives rise to the great convexity of the floor of the dorsal spiracular sac, and the tip itself lies under the sharp summit, which is marked by the opening of the nasal passage. It has already been mentioned that the wall of the spermaceti organ varies greatly in thickness. This is due to the presence of a dense mass of white, fibrous tissue which may be designated as the pillar of the spermaceti organ. This structure first appears as a small protrusion into the lower spiracular sac just dextrad of the orifice of the nasal passage. Rostrad and caudad to it are recesses, which meet below its ventral tip and together form a small pouch which constitutes a lateral dilatation of the air passage. The pillar quickly expands from its small beginning till it forms the ventral half of the wall of spermaceti organ. It is this portion of the wall which is related to the skull, the ventral spiracular sac intervening. In the continuation of its course the pillar occupies the same relative position in the wall of the spermaceti organ — that is, the ventral half — till the caudal extremity is reached.

Here, as the dextral turn is made, it passes to the caudal wall and it remains in this position in the subsequent turns. As has been said, the pillar is made up of dense, white, fibrous tissue and it is undoubtedly its presence that gives to the spermaceti organ its peculiar winding course.

The remaining portion of the wall of the spermaceti organ is comparatively thin, especially so at the rostral extremity where it consists merely of a thin, fibrous sheath forming the roof. This remains opposite the pillar

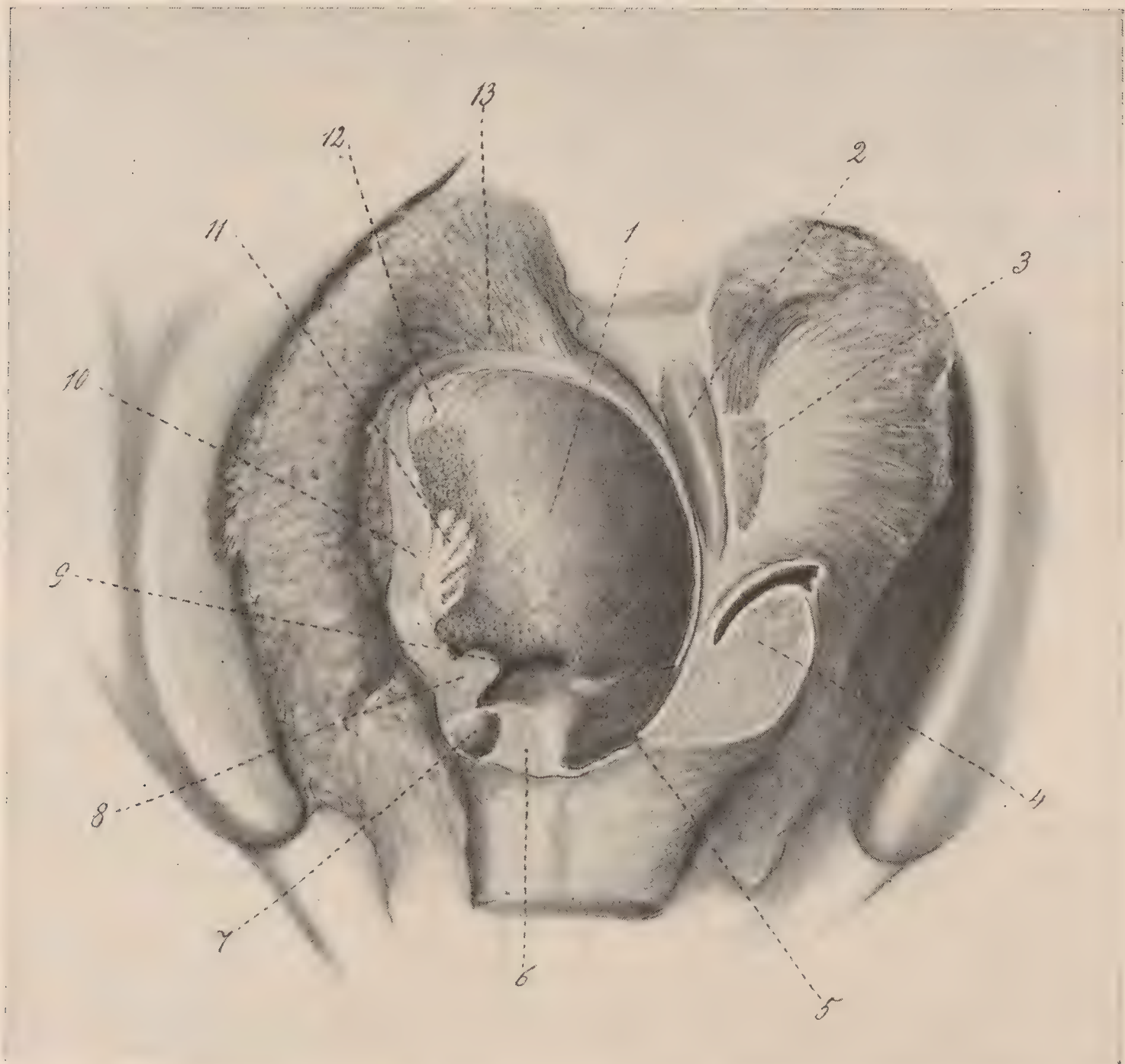


Fig. 4.— Exposure of floor of ventral spiracular sac.

1. Floor of ventral spiracular sac lying in concavity of right premaxilla.
2. Median crest, right premaxilla.
3. Muscle bundle to dextral angle of caudal lip of blow-hole.
4. Rostral wall of left air passage.
5. Wall of "case."
6. Rostral wall, right air passage.
7. Small cavity in rostral wall, right air passage.
8. Rostral tip of "pillar" of spermaceti organ.
9. Right air passage.
10. Muscular wall of ventral spiracular sac.
11. Vertical column of folds covered by papillæ.
12. Transverse folds in wall of ventral spiracular sac.
13. Deepest layer of transverse muscular sheath.

and so shifts to the rostral wall in the winding portion. In this region, however, it has become thicker, so that a cross section of the spermaceti organ at the dorsal termination shows a ring of white fibrous tissue surrounding a core of yellow fat, which is the representative of the sponge-like tissue found farther rostrad.

The second spiracular sac bears the same relation to the spermaceti organ as the pleura does to the lung: that is, it forms a cavity into which that structure is thrust, as the lung is into the pleura, with the resulting formation of visceral and parietal areas. A region corresponding to the hilum is found where the organ turns about the right nasal passage. Here the parietal and visceral layers join.

Rostrad, the sac thrusts itself between the wall of the spermaceti organ and that of the case which contains it. A sharp, free edge, which represents the point of junction of its two walls, can be seen in this position. Dorsal to the organ, it intervenes between it and the floor of the first spiracular sac. Sinistrad, it lies against the muscular wall formed by the bundles from the anterior wall of the left nasal passage; and ventrad, it forms upon the rostrum a bed in which the organ lies. To the right, along the course of the air passage running dorso-ventrad from the apex, is a considerable area which stands out clear of the sac and thus forms the hilum above mentioned.

The chamber floor upon the surface of the rostrum forms an oval area 4.5 cm. by 3.25 cm. Sinistrad, the margin of this area is convex throughout its extent. Dextrad, the margin is indented by a prominence rising from the surface of the premaxilla — due to the presence of a bony tubercle already mentioned by one of us (Schulte). It is about this tubercle, rather than about the right air passage, that the spermaceti organ turns. It is important to notice that the ventral aspect of this spiracular sac and the surface of the right premaxilla, on which it lies, are exactly fitted one to the other. This suggests that it is to the development of the spermaceti organ and spiracular sacs that the peculiar shelf-like character of the dorsal surface of the premaxilla owes its origin. We may, moreover, conclude that the variations in the contour and depth of that shelf are responses to variation in the size and shape of the spermaceti organ.

The tubercle gives origin to a number of vertical folds in the wall of the spiracular sac which extend dorsad into the elbow of the crook. Between them lie deep recesses. These folds and recesses undoubtedly serve to increase secretive or absorptive surface. They were described and portrayed by both Benham and le Danois.

The visceral portion consists of a fibrous base covered by a smooth shining layer of black epithelium. The opposing wall, on the other hand, is studded

as thickly as possible with tiny papules, which appear to have no regular arrangement and get their varied shapes from mutual compression. They are flattened on the roof of the sac, but they hang in dense masses on the sides, over the ridges above mentioned, and in the groove where the two walls join. They have been described and figured by le Danois and Benham, and their histological structure has been given by the latter. This wall varies considerably in thickness. A layer of muscle bundles from the right side of the air passage forms the bulk of the dextral and caudal portion. The muscular fasciculi are thick rostrad but become thinner as they pass caudad and encircle the pillar of the spermaceti organ, about which they form a sort of sphincter. They finally disappear in the caudal region of the wall. As they encircle the pillar they throw the inner surface of the sac into transverse folds, studded by papillæ, similar to the vertical ones already described.

The roof of this sac, which separates this cavity from the dorsal one, is also composed of encircling muscular fibres of the same origin as those just mentioned. They are of considerable thickness dextrad and caudad. Elsewhere, they are not present.

The remainder of what I have called the parietal wall of the lower cavity — that is, the portion lying upon the rostrum, and lining the wall of the case on the left — is of a thin fibrous structure.

The visceral portion of the wall of this cavity, as has been shown, lies in contact with the spermaceti organ. Rostrad, it is but loosely connected thereto and can be easily separated; but, in the curving portion and approaching the tip, it is so closely adherent that any separation is impossible.

Le Danois described a second chamber of the spermaceti organ, larger than the caudal and lying on the anterior part of the rostrum. This is not present in our specimen. But, just at the point where the right nasal passage enters the bony canal, in the anterior wall, is a tiny cavity the size of a pea. It is smooth-walled and appears to have no communication with the larger chamber. This may possibly be the as yet undeveloped anterior chamber of the spermaceti organ.

As le Danois describes these organs they are arranged in the following order counting from the blow-hole: (1) the superior respiratory sac, (2) the inferior respiratory sac, (3) the posterior spermaceti chamber, (4) the anterior spermaceti chamber. They adapt themselves to the shape of the anterior face of the skull and mutually to one another. Benham does not describe the spermaceti chambers. In our specimen, the various chambers are arranged in the order and manner that le Danois describes, except for the slight development of the anterior spermaceti chamber.

A connection which we did not find is that between the spermaceti

chambers and the respiratory passage. Pouchet and Beauregard described it for the cachalot. The evidence here at hand seems to point to the spermaceti chambers being a closed system. Le Danois says nothing on this point. Since *Kogia* and the cachalot are so closely related, if the connection were present in one we should expect to find it present in the other. Pouchet and Beauregard were very positive, saying that it is owing to the presence of the free openings from spermaceti organs into the right nasal passage that the former contained no spermaceti. We may, indeed, think of the spermaceti chambers as belonging embryologically to the nasal tract. That no open connection remains at birth in *Kogia* appears to us as certain. Confirmation of the findings in respect to this point seems desirable.

Pouchet and Beauregard remark as follows:

Il recouvre immédiatement l'organe du spermaceti, qui se présente après la dissection comme formé de deux parties distinctes: c'est d'abord en arrière un sac pyriforme adossé à la muraille verticale et concave formée par le frontal et le maxillaire accotés. Nous appelons ce sac *réservoir postérieur*. Il se continue en avant en une sorte de large boyau qui repose sur la partie horizontale du maxillaire et se prolonge jusqu'à l'extrémité de la tête. Nous appelons ce boyau, *réservoir antérieur*. Les deux réservoirs forment l'un avec l'autre un angle à peu près droit. Ils communiquent entre eux par un orifice de la largeur du petit doigt. En arrière de cet orifice, le réservoir antérieur se continue en un canal qui occupe la fosse nasale droite atrophiée comme on le sait par rapport à la fosse nasale gauche. Ce canal s'ouvre finalement dans l'arrière-cavité des fosses nasales; on ne peut mettre en doute, par suite, que les réservoirs à spermaceti soient, comme nous l'avions indiqué déjà, les représentants de la narine droite modifiée pour un usage spécial.

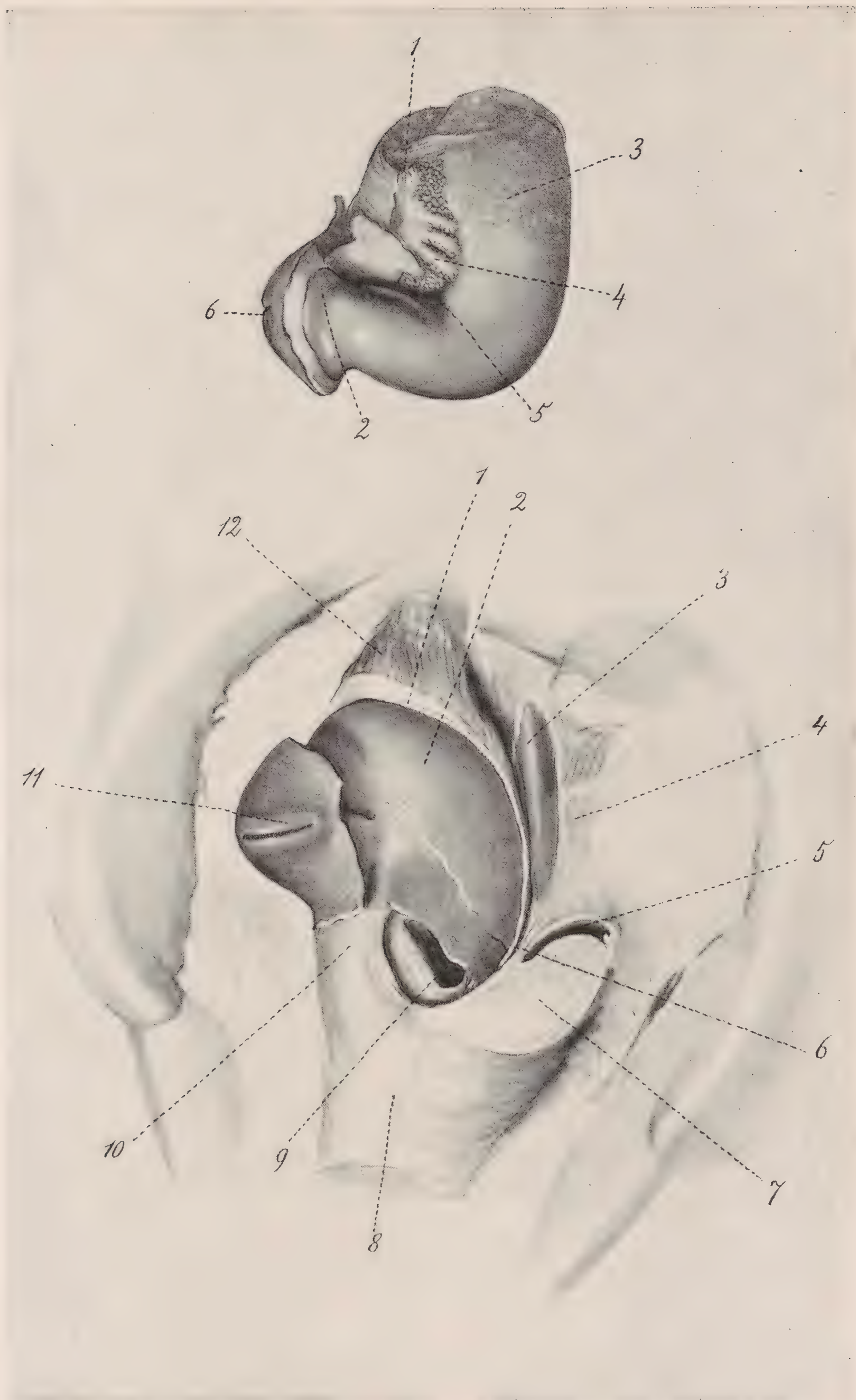
Le mode de terminaison du réservoir antérieur à l'extrémité de la tête est la

Fig. 5.—Ventral surface of the pillar of the spermaceti organ.

1. Rostral tip of "pillar" of spermaceti organ.
2. Caudal tip of pillar of spermaceti organ.
3. Ventral surface of spermaceti organ indented by papillæ.
4. Vertical folds covered by papillæ.
5. Elbow of spermaceti organ.
6. Opening of air passage.

Fig. 6.—Dorsal surface of spermaceti organ lying in its bed on the rostrum.

1. Fissure between parietal and visceral walls of ventral spiracular sac.
2. Dorsal wall of spermaceti organ covered by visceral wall of ventral spiracular sac.
3. Median crest of premaxilla.
4. Cross section of deepest layer of muscle bundles which passes to dextral angle of caudal lip of blow-hole.
5. Left nasal passage.
6. Wall of "case."
7. Rostral wall of left air passage.
8. Median raphe.
9. Open rostral end of spermaceti organ.
10. Rostral wall of right air passage.
11. Orifice of right air passage in floor of dorsal spiracular sac.
12. Layer of muscle inserting into caudal wall of ventral spiracular sac.



Figs. 5 and 6.

suisant. Ce réservoir n'est pas clos; il se termine immédiatement au-dessous de la peau, par un orifice en forme de longue fente transversale limitée par deux lèvres épaisses; cette fente s'ouvre dans une cavité sous-cutanée verticale en communication d'autre part avec l'évent. Cette *cavité verticale* s'étend beaucoup plus à droite qu'à gauche. Quand, par une incision cruciale de la peau, on ouvre sa paroi antérieure, on aperçoit l'orifice transversal du réservoir antérieur qui, avec ses deux lèvres, a l'aspect d'un *museau de singe* (1) nom que nous lui conservons.

En résumé, l'organe du spermaceti communique en avant indirectement avec l'évent, et en arrière directement avec l'arrière-cavité des fosses nasales. On s'explique ainsi pourquoi nous avons trouvé les réservoirs vides.¹

It would seem from this description that they have mistaken the orifice of the right nasal passage, designated by them as "museau de singe," for the opening of the rostral spermaceti chamber. In *Kogia*, at least, there is no connection between the two.

Some of the muscles associated with the nares have been described elsewhere² and the others have been incidentally mentioned in the course of our description of the nasal passages. For purposes of clearness, however, it seems best, in spite of the repetition, to give in one section a brief description of them all.

We could find no distinct trace of a sphincter of the blow-hole. The lips are made up of an exceedingly dense, white, fibrous tissue, in the mass of which may lie muscle bundles. We were unable to identify these, and so were drawn to the conclusion that the chief factor in closing the orifice must be water pressure. Le Danois described a sphincter and it may very well be that, as the animal advances in age, a sphincter develops.

Immediately beneath the integument and the fatty coat underlying it is a great sheet of muscle radiating in all directions from the blow-hole. It takes origin from the margins of both maxillæ, extending from near the median line caudad well rostrad to the antorbital notches. The bundles converge from this extensive origin toward the air passages, splitting into many layers. The more superficial insert into the lips of the blow-hole and evidently have the function of dilators of that orifice. Immediately beneath them is a sheet intimately related to the spiracular sac of either side. It forms a thin fibro-muscular sheath adherent to their dorsal surfaces, sends fibres among the finger-like pouches extending from their cavities, and, gathering into thicker bundles at their borders, anchors them firmly to the maxillæ.

Finally, another layer of bundles from the same origin passes, on the left side, behind the spiracular pouches and inserts into the dextral angle

¹ Pouchet and Beauregard, 1885, Note sur l'organe des spermaceti, C. R. Soc. Biol., Paris, An. 37.

² Schulte, H. von W., and Smith, M. deF., 1918, Bull. Amer. Mus. Nat. Hist., XXXVIII.

of the posterior lip of the blow-hole and the upper part of the caudal wall of the case. The upper fibres of this layer concentrate into a thick bundle, which reaches the dextral angle of the blow-hole and inserts as well into a raphe which lies between it and certain vertical fibres of the wall of the case now to be mentioned. These fibres take origin with those composing the rostral wall of the left nasal passage. They pass around the mesal angle of the canal, caudad to the bundle just described, turn dorsad, and insert into the raphe just mentioned and the dextral angle of the blow-hole. The action of these muscles would be to fix and retract the caudal lip, and perhaps to move it sinistrad.

The bundles related to the nasal passages take origin from the dorsal surface of the rostrum in the midline, from a median raphe, and from the mass of tissue covering in the rostral end of the spermaceti chamber. On the left side, they form the great mass of the rostral wall of the air passage, as described in connection with that structure. On the right side, also, they form the rostral wall of the air passage, but the bulk of the fibres pass about its lateral angle and form the thick muscular wall and the periphery of the roof of the ventral spiracular chamber. These walls thin out as they pass caudad, the muscle bundles finding insertion in the fibrous sheath of the wall. It has already been mentioned that the more dorsal of these fibres encircle the pillar of the spermaceti organ and the right nasal passage in the manner of a sphincter.

The bundles originating in the fibro-areolar mass about the rostral end of the case and those from the caudal portion of the raphe form the walls of the case as has already been described. When the mass of the snout is removed, it is the cut edges of these fibres which form the arch about the rostral extremity of the spermaceti organ.

LARYNX

Benham has given a very complete and adequate description of the larynx of *Kogia*, and we find little to add to his description. We shall be content, then, with mentioning the few particulars in which our specimen appears to differ from his and omit a detailed description.

We have already mentioned the manner in which the laryngeal tube rises from the pharyngeal floor and protrudes into the naso-pharynx, where its thickened tip is closely embraced by the areus palato-pharyngeus. This arrangement is one which *Kogia* shares with other odontocetes. Le Danois gives an excellent cut showing the embracing collar. On dorsal view, a decided asymmetry is apparent, the left side of the larynx being flattened, due doubtless to the sinistral displacement of the whole structure.

The extrinsic muscles have been described in another section. As concerns the intrinsic muscles, in certain respects our animal differs from that of Benham. First, as to the crico-thyroid muscle: Benham described and pictured this as a small slip lying mesad to the posterior cornu of the thyroid cartilage and entirely concealed from view by that structure and a mass of muscle arising therefrom. This slip we failed to find. In its place was a bundle taking origin from the mesal surface of the cornu and inserting into the arytenoid near the muscle process. This band appears to be that which Benham described as crossing the bay between the cornu and the body of the thyroid cartilage. Its action, with the thyroid cartilage fixed, would be to pull the arytenoid away from the epiglottis: in other words, to open the larynx.

The crico-arytenoid muscles, lateralis and posticus, are arranged as Benham described. It is to be remembered that the arytenoids in the cetacean have lost their rotary motion and move in only two planes, the sagittal and coronal; so the crico-arytenoid lateralis muscle has shifted dorsad and no longer serves to rotate the ventral end of the cartilage outward, but acts as an opponent of the inter-arytenoideus which approximates the cartilages. The more dorsal bundles perhaps assist the posticus in turning the arytenoids dorsad, thus opening the larynx.

These three muscles then act as a group to retract the arytenoid cartilages from the epiglottis.

The inter-arytenoideus muscles have the usual arrangement, passing between the dorsal surfaces of the two cartilages and, in their action, approximating them.

We find the hyo-epiglottic muscles arranged as Benham pictured them, passing from the dorsal surface of the hyoid bone and finding insertion in the venter of the epiglottis midway from the extremities. They have a direct pull forward on that structure. We can not analyze the muscles opposing the retractor group in the same manner as Benham did. Taking origin from the outer surface and ventral edge of the base of the arytenoid and passing ventrad to the angle between epiglottis and thyroid plate is a mass of muscle which that author divided into three. The most dorsal bundle he called thyro-epiglottic. We do not find the insertion he gave it on the epiglottis. The bundle next caudad, according to him, extended from ventral margin of the arytenoid to the dorsal edge of the epiglottis. He called this the ary-epiglottic. Finally, a third bundle passed from base of arytenoid to entel surface of thyroid plate. As we said above, it appears to us that the dorsal connection of all these bundles is the base of the arytenoid. The ventral connection is the ventral surface of the caudal extremity of the epiglottis, a few fibres passing to the thyroid. So perhaps a better designation of the muscle would be aryteno-epiglottic.

However these muscle groups are analyzed and designated, their action is clear and comparatively simple. The hyo-epiglottic and crico-arytenoid group open the laryngeal passage, separating arytenoid and epiglottis. The inter-arytenoid muscle approximates the arytenoids, and the crico-arytenoid muscles oppose this action.

We have nothing to add to Benham's account of the cartilages. The divided thyroid is as he described it. In this specimen, the tubercle of the epiglottis, where it juts ventrad between the thyroid plates, is much more prominent than he pictured it. His analysis of the arytenoid cartilage is of great interest and, for it, we refer to his original account.

TRACHEA AND BRONCHI

The trachea, owing to the collapse and elongation of its walls by stretching, is not in condition to furnish accurate measurements. Its shape, moreover, can not be accurately ascertained. It appears to have a tendency to take the contour of an hour glass on cross section, with longitudinal grooves on either side. Its length to the bifurcation is 4 cm.; to the origin of the eparterial branch on the right side, 3 cm., this branch being thus tracheal in origin. The length of the eparterial branch is 2.5 cm. from its origin to its entrance into the substance of the lung, just short of which point it gives off another branch to the apex. The right main bronchus is 2 cm. long. As for the left main bronchus, it has a total length of 5 cm., of which 2 lie caudad to the first branch.

The trachea measures 2 cm. in its greatest diameter; the right main bronchus, 1.25 cm.; the left main bronchus, 1.5 cm. The striking thing about these measurements is the relative width of the trachea and the great proportional length of the stem bronchi. This latter is due to the hilum of each lung being a deep recess, comparable to the hilum of a kidney. Only in the depth of these recesses do the bronchi actually enter lung substance. The arrangement of the eparterial branch on the right side points to a greater functional importance of that lung. This is another indication that the smaller measurements of that lung are, as is noted below, due to the unequal distribution of blood (*post mortem*).

From the ventral aspect, the trachea appears to have eight rings, of which the first has twice the breadth of the others. On the dorsal aspect, the rings are complete and are united by cross strands in groups of four, thus forming two compound rings. Each main bronchus, just caudad to the bifurcation, has one broad complete ring, then a number of narrow ones as far as the entrance into the lung substance. All of these rings

are complete. Investigation of the histological structure of the trachea and bronchi was not undertaken, nor was their arrangement within the lung investigated.

THORAX

The thorax is rather broad ventrally in correspondence to the width of the sternum. Dorsad, its transverse diameter increases for about two-thirds the length of the ribs, contracting again in the region of the deep pulmonary grooves. On account of the flaccidity of the parts, the following dimensions are but approximate and, of course, represent proportions in an unexpanded chest:

	<i>cm.</i>
Length along ventral midline.....	12.5
Length dorsally, right side.....	27.0
Length dorsally, left side.....	26.0
Width between fourth ribs.....	11.5
Depth at level of fourth ribs, sternum to spine.....	8.5
Ditto, sternum to pulmonary groove.....	13.5

The plane of the superior aperture is very oblique, its dorsal limit, the neck of the first rib, standing 6 cm. rostrad of the margin of the sternum. The form of the opening in the soft parts is subrectangular and measures about 7 cm. dorso-ventrally by 5 cm. transversely. The unusual contour is due to the presence of a large, vascular fat pad which fills the concavity of the ribs, extending into the interval between the scalenus and small longus colli muscles and caudal as far as the third rib; its ventral limit coincides with the line of pleural reflection and dorsally it reaches the pulmonary groove.

The diaphragm has the usual extreme obliquity observed in cetaceans. The caval orifice lies at the level of the sixth thoracic vertebra. From this point the diaphragm slopes ventrad as well as dorsad. The ventral slope corresponds to the heart and pericardial fat pads and reaches the ventral body wall at the end of the sternum. The dorsal slope is much longer, extending to the fascia of the hypaxial muscle mass at the level of the third lumbo-caudal vertebra.

The topography of the thoracic viscera is peculiar in the extensive apposition and adhesion of the mediastinal contents to the thoracic wall. The thymus and pericardium are attached in the whole extent of the sternum and costal cartilages and for a considerable, distance upon the ribs. The pleuræ are, in consequence, widely separated, and the lungs are distinctly dorsal to the heart and do not overlap it at the sides. Dorsally, there is

further evidence of this ventral gravitation of the mediastinal viscera in the wide separation of aorta and œsophagus towards the diaphragm. The latter organ retains its relation with the pericardium and is suspended in a broad fold like a mesentery, formed by the approximation of the two pleural sacs.

PLEURA

The dome of the pleura extends but a short way into the neck, rising to the upper border of the first rib in the region of its neck, but, on account of the obliquity of the ribs in the uninflated thorax, this point lies 6 cm. beyond the rostral margin of the sternum. The dome by no means fills the wide interval between the scalene and longus colli, which is mainly occupied by adipose tissue containing a highly developed rete mirabile. Ventrad, the parietal pleuræ are widely separated by the mediastinal complex, which is very broadly adherent to the thoracic wall. The line of pleural reflection is displaced farther on the left than on the right, but on neither does it anywhere reach the sternum. Its course is peculiarly modified by the folds associated with the pericardial fat bodies. These latter are of crescentic shape, attached ventrally in the line of junction between fibrous pericardium and diaphragm, and thence extending upon the thoracic wall at the caudal limit of the area of pericardial adhesion in a transverse direction, on the left side, to a point on the third rib 3 cm. from its cartilage and, on the right side, in the second space about 1 cm. farther ventrad. Correspondingly, a fold of parietal pleura is formed, its base attached in the area described and turning a free edge dorso-mesad towards the lung in the interval between the base of that organ and the diaphragm. The pleural cavity is thus partially subdivided ventrally on a level with the highest part of the diaphragm; and the incomplete partition is located, with reference to the lung, just caudal to its region of greatest breadth, at the beginning of the long tapering prolongation which rests upon the dorsal slope of the diaphragm. The folds in the specimen are flaccid from the dissolving of the fat during a long period of preservation, and, caudally, there depends on each side a long free process into the caudal portion of the pleura.

The two pleural sacs converge from their domes towards the thoracic aorta, which begins at the fifth thoracic vertebra. The line of reflection of the right sac crosses the aorta obliquely and from the seventh vertebra caudad to the diaphragm the sacs are in contact, forming the broad fold (described above) which extends to the œsophagus. On the diaphragm the lines of reflection are widely separated by the pericardium and its fat bodies, on account of which the pleural reflection at first runs dorsad on the thoracic

wall of the third rib at some distance from its extremity and then turns rostrad along the ventral limit of the thoracic fat pad to the dome, crossing the first rib at a point rather nearer to its angle than its extremity. Thus the pleuræ cover only a narrow area of the fibrous pericardium near its dorsal limit and altogether fail to reach thymus, or sternum, or its attached cartilages.

The visceral pleura requires no special comment. The ligamenta lata are broad and extend to the diaphragm. Mesad, they join the sides of the aorto-oesophageal fold dorsal to the oesophagus.

LUNGS

The lungs, compressed from side to side conformably to the deep costo-vertebral groove, have considerable dorso-ventral height. The apices, retaining this compressed form, are roundly curved in profile, and, mesially, each has a shallow groove for the posterior thoracic vessels. The lung broadens from the apex to the junction of pericardium and diaphragm, thence narrows at the expense of its ventral portion, and caudally runs out into a tapering point. The diaphragmatic surface is defined by sharp margins, which become rounded and obscure when the pericardium is reached, so that here and rostrad the compressed lung can be described as having a costal and a spinal surface; and thick dorsal and ventral margins, the latter apposed to the pericardium where it is not occupied by the hilus. The left lung is deeply grooved in its upper portion by the arch of the aorta. Le Danois has noted the rounded apex and pointed extremity of the lung of *Kogia*; in his specimen, the right lung was much the larger. In this foetus, there is a remarkable reversal of usual proportions, for the left lung is larger than the right. It is, however, engorged with blood, as shown by its darker color and firmer consistency throughout, and its otherwise incomprehensible dimensions are probably to be assigned to this.

Measurements of Lungs

	Right	Left
	cm.	cm.
Total length.....	17.8	19.8
Length of diaphragmatic surface.....	11.6	14.8
Greatest thickness.....	3.5	3.4
Greatest dorso-ventral diameter.....	5.7	6.1

PERICARDIUM

The fibrous pericardium is bluntly conical, having a wide rostral termination upon the great vessels on account of their huge size and, caudad, being

broadly adherent to the diaphragm. Ventrad, it is broadly adherent to the thoracic wall and also at the sides, for the mediastinal pleura is reduced in extent and has but a narrow contact with the pericardium. The serous layer resembles that of *Balænoptera* and shows the same evidences of sagittal shortening in the narrow circular sinus and the total reduction of the oblique sinus.

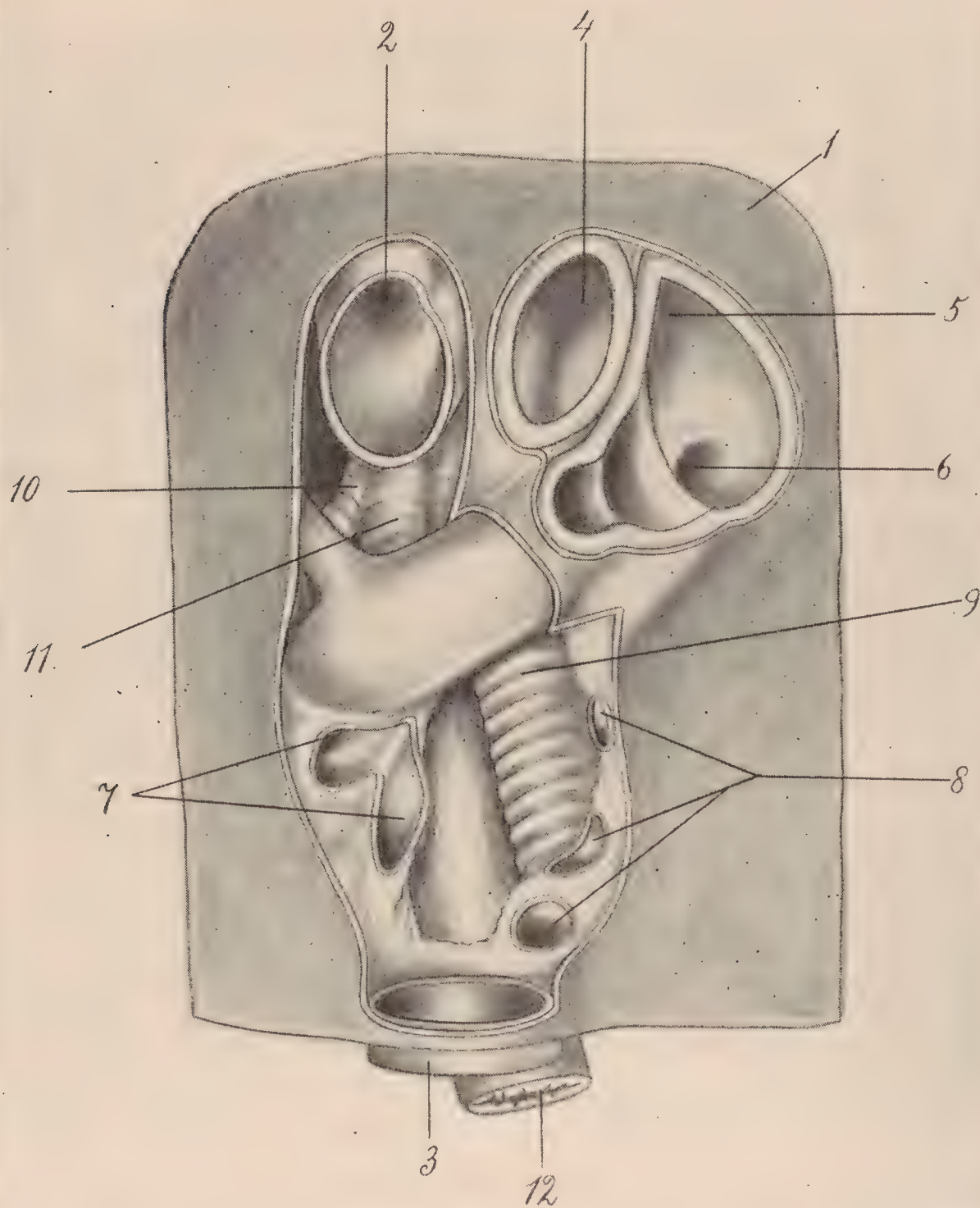


Fig. 7.—Interior of pericardium, showing reflection of serous layer and exposure of mediastinal structures in relation to its dorsum.

1. Fibrous pericardium.
2. Precava.
3. Postcava.
4. Aorta.
5. Pulmonary artery.
6. Ductus arteriosus.
7. Right pulmonary veins.
8. Left pulmonary veins.
9. Left primary bronchus.
10. Tracheal bronchus.
11. Right primary bronchus.
12. Oesophagus.

HEART

Le Danois has described briefly and illustrated the heart of the adult, calling attention to its great breadth, the high relief of the columnæ carneæ of its ventricles, the great size of aorta and pulmonary artery, and the absence of the corpora aurantii on the sigmoid valves, and noting the character of the atrio-ventricular valves and the papillary muscles. This heart corresponds to the conditions described, allowance made for the foetal condition.

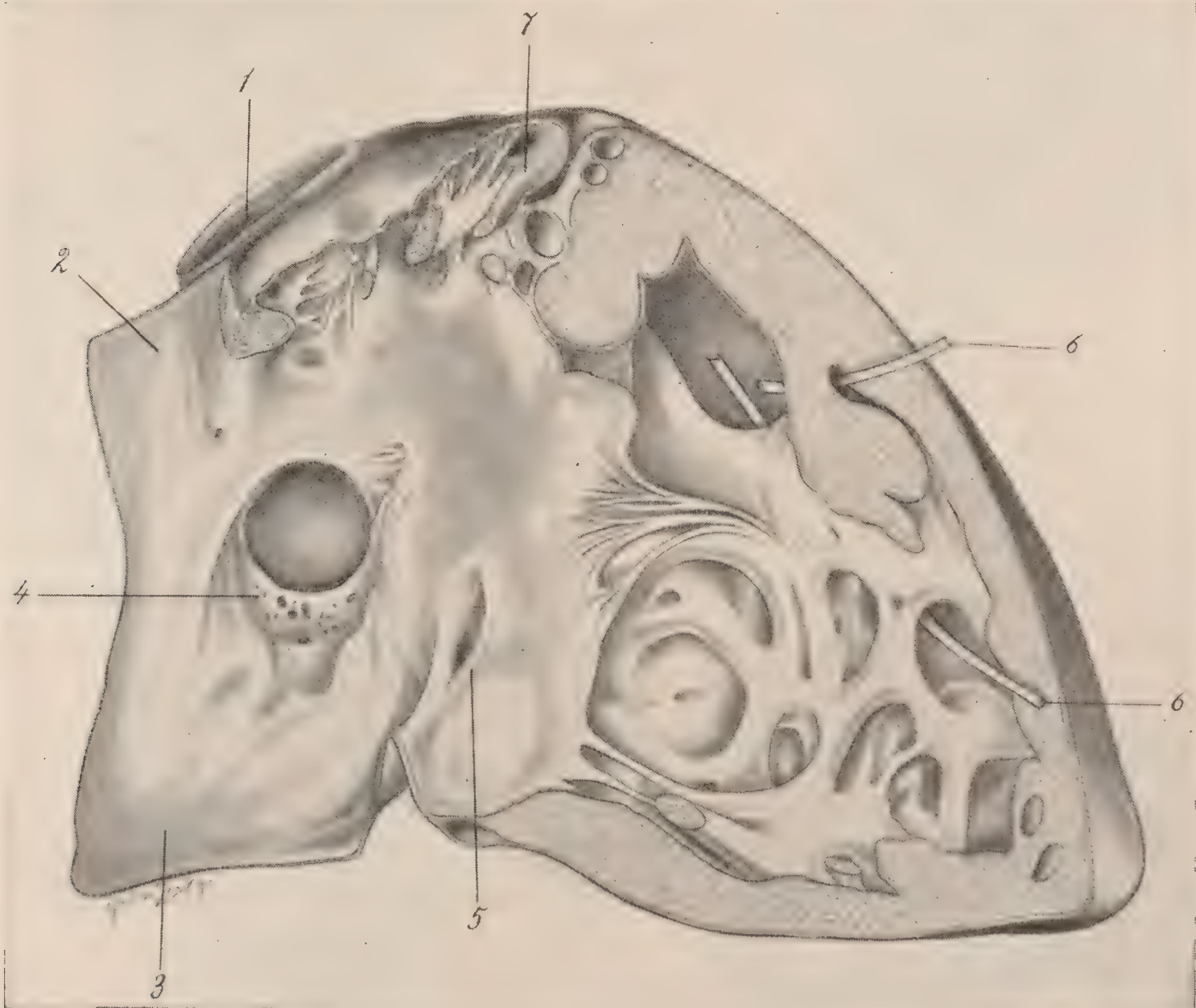


Fig. 8.—Sagittal section of right auricle and ventricle.

1. Aorta.
2. Precava.
3. Postcava.
4. Valvula fossæ ovalis.
5. Thebesian valve.
6. Probes passing under columnæ carneæ into conus.

It is placed with more of its bulk to the left than to the right of the median line; its long axis is slightly oblique, and a small degree of rotation has taken place, as the area of right ventricle in its sterno-costal surface exceeds that of the left. Unfortunately, the organ is somewhat deformed

by a bending dorsad of the sides of the ventricles which prevents accurate measurement. The apex is obscurely notched.

The auricles are peculiar in the incomplete amalgamation of their atrial and venous portions. The sulcus terminalis on the right side is deep and complete, especially at the orifice of the postcava where its internal projection forms a high ridge in the position of and clearly has the function of the Eustachian valve. The ridge is continued to the limbus ovalis, where it forms the dorsal limit of the orifice of the coronary sinus. A well developed Thebesian valve extends from the ventral aspect of this ridge to the septum atrio-ventriculare guarding the orifice of the coronary sinus, as is usual in mammals but not in Cetacea where these structures are early reduced.¹ One further detail deserves comment. Between the orifice of the postcava and the ventricle there is an oval area, about 1.5 mm. by 1.25 mm. in extent, where the auricular wall is so tenuous as to be translucent and bulging. This area may be precisely located: it extends sagittally from the terminal ridge to the right coronary vein, and transversely from the Thebesian valves to the junction of the floor and right wall of the auricle. A possible explanation of this peculiar condition may be sought in the failure of complete amalgamation of the two embryonic constituents of the auricle, for the sinus valves owe their inception to the telescoping of the sinus venosus into the primitive atrium. This process, being retarded and markedly so adjacent to the postcava, expresses itself in the substitution of the terminal ridge for the Eustachian valve and indicates that the larger moiety of the right sinus valve has here persisted as part of the auricular wall, instead of being invaginated as usual to form the duplicature which gives rise to the valve.

The foramen ovale is large, measuring 18 mm. sagittally by 16 mm. dorso-ventrally. The annulus is prominent and well developed. The

Fig. 9.— Tongue, oropharynx, nasopharynx, larynx, and œsophagus. The alimentary passages are opened by a dorsal median incision; the right half of the nasopharynx has been removed.

1. Tongue.
2. Oropharynx.
3. Œsophagus.
4. Nasopharynx.
5. Velum palati.
6. Arcus palato-pharyngeus.
7. Larynx.

Fig. 10.— Plicate organ and crypts of the nasopharynx, left side. Below is the arcus palato-pharyngeus, the "repli en collerette" of le Danois.

Fig. 11.— Thymus, ventral view. One-half natural size.

¹ Turner, W., 1872, An account of the great finner whale stranded at Longniddy (*Balænoptera Sibaldii*), Trans. Roy. Soc. Edin.

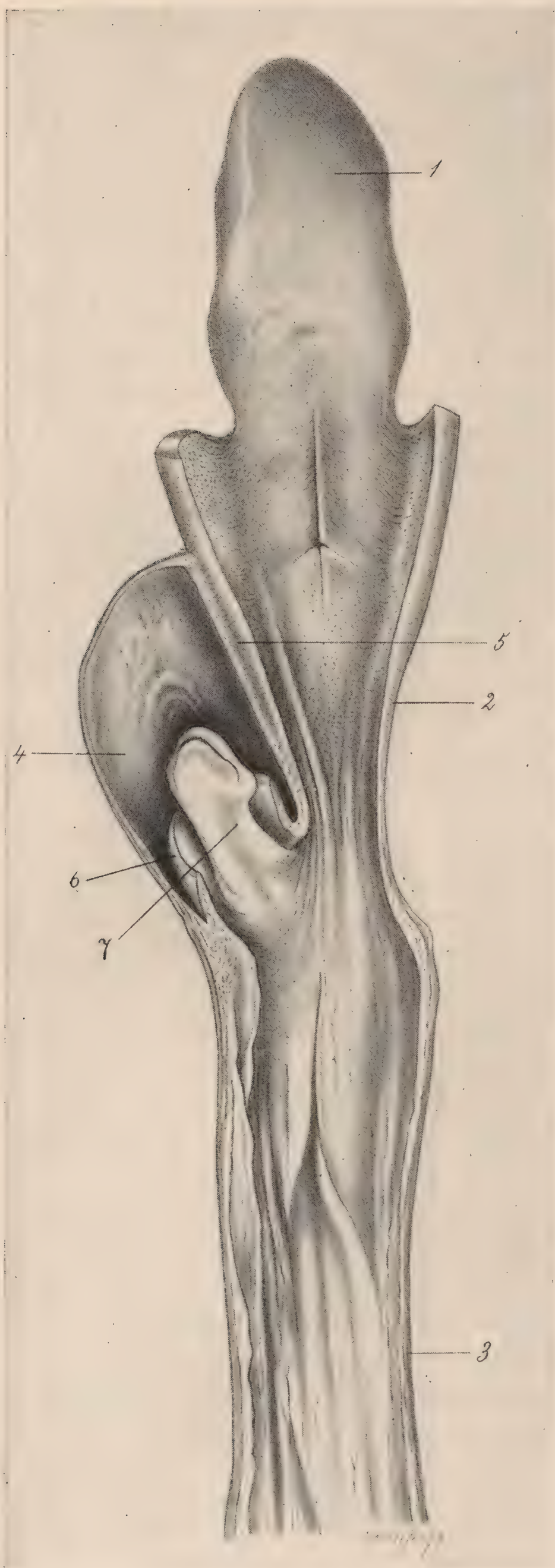


Fig. 9.

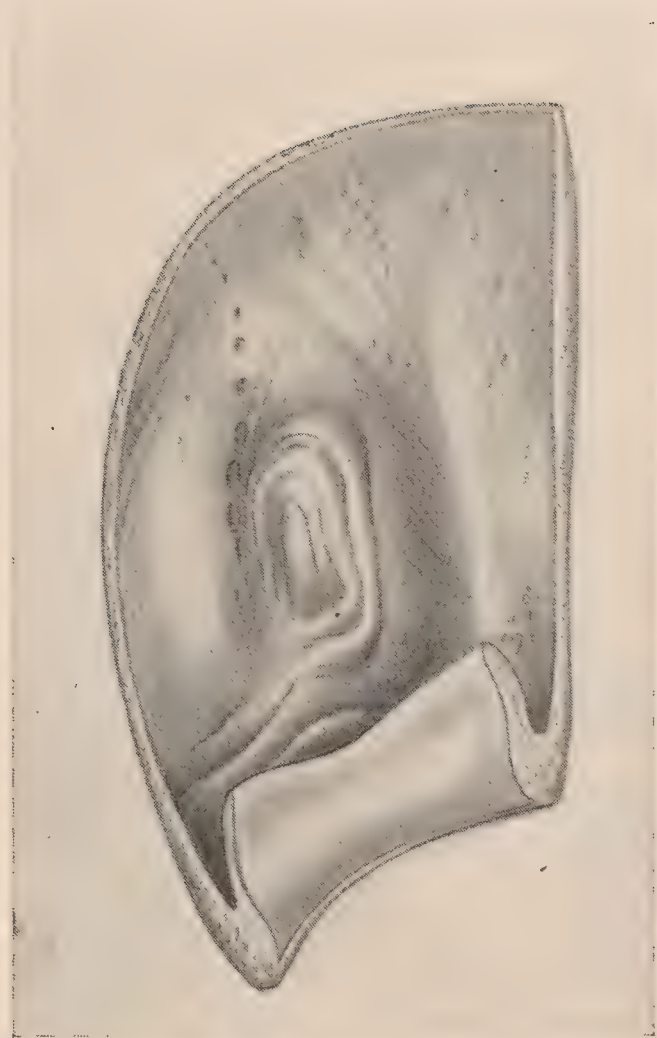


Fig. 10.

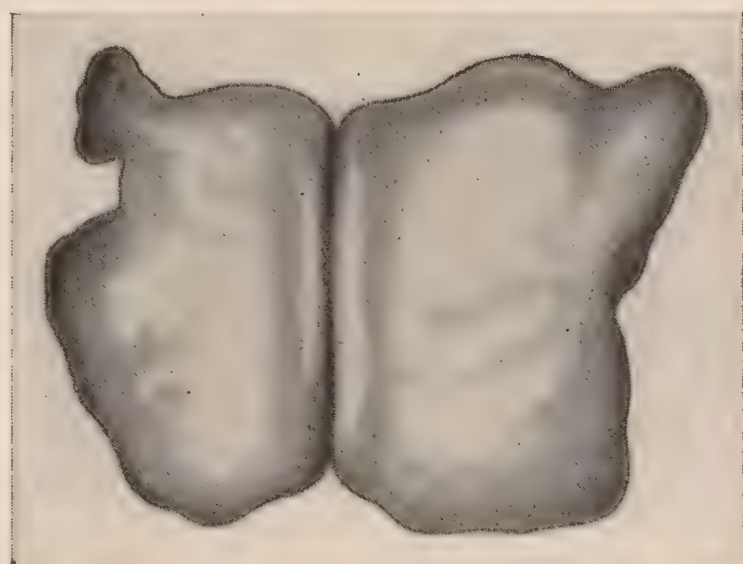


Fig. 11.

valvula seems adequate to effect complete closure were it not for its extensive fenestration, for in much of its extent it abounds in minute but close set perforations. Its line of attachment coincides with the limbus caudally, but its dorsal cornu deviates more and more to the left, being carried into the left auricle and terminating fully a centimeter to the left of the limbus. The ventral cornu has an analogous deviation in the opposite sense — being carried to the right of the auricular septum and here folded upon itself, to judge by the relief of the septum which, above the extremity of the valvula over a triangular area, has a cribriform appearance as though the fenestrated valve had secondarily become adherent. If the interpretation of this area is correct and it does represent the tip of the ventral cornu of the valvula, then it may be said that the cornua of the valve have extended around the whole circumference of the limbus and would have met in this foetus had not the dorsal cornu deviated to the left. This observation is of some interest in connection with the thimble-shaped valvula of *Balæna*,¹ *Balænoptera* (according to Turner), and *Megaptera* being attached to the limbus in its whole periphery and allowing the passage of blood to the left auricle only through its perforations. The valve of *Kogia* throws some light on the evolution of this form, which could be derived by the enlargement and fusion of such cornua as here described, could their extension have occurred in one plane. In both types there is the same great size of the valvula, its fenestration, and its ballooning into the left auricle; in all of which, the known mystacocetes have advanced beyond *Kogia*.

The left auricle shows the same incomplete amalgamation of its component parts; a deep sulcus terminalis, if the term may be used of the left auricle, descends beside the left pulmonary veins. In consequence, these veins, together with the short trunk of the right side, open into a convex sac at the back of the atrium; this is widely confluent with the auricle proper between the ridge corresponding to the terminal sulcus and the valve of the fossa ovalis.

The atrio-ventricular valves have the usual flaps and those of the tricuspid are at least as well developed as usual; this is stated because le Danois found the tricuspid valve in his specimen “représentée par un repli solide membraneu.” Of the papillary muscles of the right ventricle, the posterior alone has anything of the form suggested by its name. The chordæ tendinæ going to the septal muscle are inserted into a depression in the surface of a large fleshy ridge which in its further course becomes undermined and a probe may be passed under it from the general ventricular

¹ Knox, R., 1838, Catalogue of Anatomical Preparations of the Whale. Edinburgh. Quoted by Turner, *loc. cit. ante*.

cavity into the conus. The lateral papillary muscle, similarly, is represented only by a portion of a ridge on which chordæ tendinæ insert. This ridge also has a free portion which joins the ridge associated with the septal papillary muscle, constituting a moderator band. All of these muscles are placed at the junction of the middle and upper thirds of the ventricle. Those of the left ventricle are somewhat more projecting and occupy the usual position in the intervals of the flaps of the mitral valve. As le Danois has noted, the wall of the left ventricle is much thicker than the right — and this is striking as regards the compactum, but the massive development of the columnæ carneæ, especially on the right side (which le Danois has also noted), renders the disparity in thickness not greater than is usual in mammals. Owing to the large size of the trabeculæ in the right ventricle, the approach to the conus is subdivided into several passages. On the left side, the vestibule of the aorta is not so obstructed; trabeculæ are numerous but of moderate size and do not stretch across the cavity to so great an extent as on the right side.

THYMUS

This organ is represented by bilateral bodies which are asymmetrical in their rostral portions, the left exceeding the right in size. They are placed against the pericardium behind the manubrium sterni and extend into the root of the neck, under cover of the infrahyoid muscles and resting upon the great vessels. Neither is in contact with the pleura. The left innominate vein grooves them dorsally, and its junction with the vessel of the right side and the beginning of the precava are similarly related to the right thymus. Beyond the veins, the thymus comes in contact with the branches of the aorta; on the right side, an oblique process is given off which rests against the concavity of the brachiocephalic and subclavian arteries; on the left side, the corresponding process is larger and fills the wide interval between common carotid and subclavian. It is in the development of these processes that the asymmetry between the two halves of the thymus chiefly consists, and this asymmetry is evidently to be referred to inequality in the reduction of the cervical portions of the two sides. The dimensions are as follows:

	Right	Left
	mm.	mm.
Length sagittally along mesial border.....	46	42
“ obliquely to extremity of process.....	57	66
Breadth.....	40	34
Thickness.....	7	8

THYROID

The thyroid body is broad and thin, resting against the thyroid and cricoid cartilages, the upper rings of the trachea, and, on each side, upon the jugular vein. The rostral margin is nearly transverse with a median concavity. The lateral lobes are somewhat prolonged caudally and acutely angled. Between them is a wide shallow notch. This notch and the concavity of the rostral margin serve to define an isthmus, which is not greatly shorter sagittally than the lateral lobes. The capsule is thick and contains a rich vascular plexus. The substance of the body is very soft; this and its thinness are presumably due to the action of the preservative. Its dimensions are:

	<i>mm.</i>
Lateral lobe, right, sagittally.....	40
“ “, left, “.....	40
Isthmus, sagittally.....	28
Transverse diameter.....	37
Thickness.....	1 to 3

At each lower pole, within the capsule, was found a small oval body of firm consistence, measuring about 7 mm. by 4 mm. These are probably parathyroids.

TONGUE

The tongue is firm and muscular. The dorsum is flatly convex, the tip rounded, and the margin uniform and well defined. The frenulum is short and thick, and rostrad of it, on the free under surface of the tip, is a depressed triangular area of slightly darker hue than adjacent parts. Caudad, the tongue sinks rapidly to the level of the alveolingual region. This conformation seems very similar to conditions observed in *Balænoptera* and is presumably to be referred to a retarded development of the radix linguæ. In *Kogia*, this portion of the tongue is situated between the arcus palatoglossi; and, on the surface, there is no demarcation between the tongue and the floor of the oropharyngeal passage. The genio-glossi, however, stop abruptly; and their sharp junction with the fibrous coat of the oropharyngeal passage is taken as the caudal limit of the tongue. From this to the tip, it measures 105 mm.; its greatest breadth is 32 mm.; the free portion has a length of 17 mm. Rostrad, the surface of the tongue is perfectly smooth. In its middle third, the punctate orifice of glands appear and become very numerous caudad. Here also, the tongue presents a median fissure of

about 2 mm. depth, which terminates behind in a triradiate figure. Few and shallow transverse furrows are given off from its sides.

OROPHARYNX

The oropharyngeal passage is long and narrow; its lumen is dorso-ventrally flattened (le Danois). The wall is very thick in the region of the arcus palato-glossus; but, caudal to this for a distance of 2.5 cm. until the pterygo-pharyngeus is reached, it is thin and poorly supplied with muscle. Entally are numerous longitudinal ridges. These all continue into the pharynx. The passage on the left, very narrow as le Danois describes it, appears more as a lateral addendum than as an actual portion of the pharynx. Le Danois describes the median ventral sulcus bifurcating in a V and sending one branch into the left passage, the other continuing into the œsophagus. This arrangement is not present in our foetus. Everywhere upon the ridges are the punctate orifice of glands.

The tonsils are represented by two crypts, one on each side, and dorsally placed in the oropharyngeal passage close to the median line. This position of the tonsil was ascertained of *Phocæna* by Rapp. The orifices of the crypts are slit-like, curved like an *f*, and measure 5 mm. in length. They each lead into a little pocket of about the same depth, which is directed dorsad and laterad. There are no conspicuous lymph follicles.

PHARYNX

The pharynx consists of a dorsal naso-pharynx and a ventral portion which receives the oropharyngeal canal. Separation between these cavities is effected by the lengthened velum and the strongly developed arcus palato-pharyngei. The latter form a short tube — *repli en collerette* — closely embracing the epiglottis and arytenoids; it is well shown in le Danois' figure.

The naso-pharynx, at first embraced between the pterygoid and otocranial plates of the occipital, rests dorsally against the basis cranii and ventrally upon the velum which is stretched between the bones mentioned. As they diverge caudad, it increases in breadth, attaining its maximum diameter between the attachments of the stylopharyngei.

The surface of the mucous membrane shows the orifices of numerous small glands which are everywhere present. In addition, there are many large crypts, such as are usually associated with the presence of adenoid

organs. In the floor, they are abundant rostrad and are grouped in double or irregularly treble rows separated by strips of smooth mucosa. In the lateral wall is a curious arrangement of low folds of the mucosa. The first of these is parallel to the arcus palato-pharyngeus, from which it is separated by a row of large crypts. On the left side, it terminates rostrad by joining the arcus; on the right, it is less prominent and gradually fades out. A second fold, at first parallel to this, on reaching its rostral extremity curves ventrad and then ascends sharply on the lateral wall. In the concavity of its curvature are several similar but loop-like folds forming an oval structure measuring 16 mm. by 9 mm. On the right side, all of these folds are less developed and those of the plicate structure are indicated only by scattered crescentic grooves like nail prints in miniature. This organ presents not a little resemblance to the human pharyngeal tonsil, as depicted by Sklabounos,¹ and is probably its homologue notwithstanding its lateral position and asymmetrical development.

The muscular wall of the pharynx is well developed and of complicated structure. We record our findings without attempting a complete morphological analysis, which is hardly possible without more detailed knowledge than is at present available upon conditions existing in other odontocetes.

The inferior constrictor (thyreo-pharyngeus) is a large muscle, divisible into caudal and rostral portions. The former portion arises from the dorsal margin of the thyroid cartilage, its caudal cornu here encroaching upon the lateral surface. Its fasciculi spread out with a rostral inclination, eventually becoming transverse to join those of its antimere in the dorsal midline of the pharynx without the interposition of a raphe. Caudad, this muscle is continuous with the superficial layer of the œsophagus. These bundles are transverse in direction; they surround the œsophagus like a constrictor as far as the thorax, but there the caudal fasciculi of the layer assume a sagittal direction and blend with its longitudinal coat. The rostral portion of the thyreo-pharyngeus is thicker, more coarsely fasciculated, and partially overlaps the caudal portion, being the most superficial of the pharyngeal muscles. It arises from a large triangular area on the lateral surface of the thyroid cartilage, occupying the region between its rostral and dorsal margins and the attachment of the sterno-thyroid. From this origin, it passes as a thick ribbon of parallel bundles to join its fellow in a feeble raphe which permits much digitation and some continuity between the fasciculi of the two sides. It covers the junction of the caudal portion of the thyreo-pharyngeus with the pterygo-pharyngeus and is so located with reference to the spout-like prolongation of the larynx within

¹ Sklabounos, G. L., 1908, *Anatomike tou anthropou*. II, fig. 89. Athens.

the naso-pharynx as to reinforce the arcus palato-pharyngeus in its rôle of preventing the entrance of water from the œsophagus into that cavity. This muscle was mistaken by Benham (who had but stumps attached to the larynx he so carefully described) for the thyrohyoid, which entailed another slight error, hardly to be avoided in the circumstances, in his diagnosis of attachments upon the thyroid cartilage. His sterno-thyroid is correct (cf. his plate xxvi, fig. 6), but the muscle ventral to it (leadered) is the true thyro-hyoid and not an accessory slip. The direction of bundles for all these muscles in his cut corresponds with our findings and the unleadered dotted area on the dorsal margin corresponds closely to the origin of the caudal part of the inferior constrictor as we find it.

The stylo-pharyngeus arises from the stylohyal mesially and nearer the skull than the styloglossus. It is a medium-sized muscle which expands to its insertion upon the lateral wall of the naso-pharynx between the pterygo-pharyngeus and the palato-pharyngeus. The naso-pharynx is dilated transversely, and its major diameter lies between the insertions of the stylo-pharyngei.

The rostral portion of the pharynx — the naso-pharynx — has a thick muscular wall, the fasciculi of which have a general longitudinal direction. A dorsal muscle arises from the pterygoid entally as far as the margin which abuts upon the basi-sphenoid. The fasciculi converge from the two sides and meet in a dorsal raphe, which terminates at the margin of the caudal segment of the inferior constrictor and is covered superficially by the rostral section of that muscle. Laterally, the pterygo-pharyngeus extends to the insertion of the stylo-pharyngeus, beyond which it blends with the palato-pharyngeus.

This latter arises from the velum palati and, by its deeper layer, also from the ental surface of the pterygoid bone. The deep layer completes the investment of the naso-pharynx with longitudinal muscle, some of its bundles meeting the stylo-pharyngeus in an inscription, some passing ventrad of that muscle to the border of the caudal division of the inferior constrictor to which they are united by a tendinous line. These latter blend dorsally with the pterygo-pharyngeus. Ventrally, the bundles arising from the velum make a strong muscular arch on each side of the junction of the bucco-pharyngeal passage with the pharynx. This forms the substance of the arcus palato-pharyngeus, which closely surrounds the spout-like prolongation of the larynx.

The superficial portion of the palato-pharyngeus arises exclusively from the fibrous tissue of the velum. It is directed caudad and ventrad to the angle between the arytenoid and thyroid cartilages, and, expanding widely, is inserted into the ental surface of the latter. From its deep surface,

a flat band of fasciculi is given off which sweeps dorsal to the under surface of the rostral division of the inferior constrictor, with which it unites in part by the interposition of a linear inscription.

ŒSOPHAGUS

The œsophagus measures 12.25 mm. from the cricoid cartilage to the diaphragm. It is distinctly displaced to the right at its commencement and rests against the right side as well as the dorsum of the trachea. The trachea of this specimen is prominent and keeled, and, by its sharp convexity, indents the œsophagus. Accordingly, this organ has a kidney-shaped cross-section, with a convex dorso-dextral and a concave sinistro-ventral wall. The œsophagus inclines to the left as far as the arch of the aorta, which displaces it again towards the right; thence to the diaphragm, it gradually regains a median position. The maximum external dimensions, just rostrad of the aortic arch, are 23 mm. transversely, 11 mm. dorso-ventrally. At the bifurcation of the trachea, the œsophagus alters its form and, projecting ventrad to a slight degree in the angle between the primary bronchi, becomes flattened from side to side. At the diaphragm it measures 18 mm. dorso-ventrally and 9 mm. transversely. The wall has a thickness of 3 mm.

Inside, the mucosa is thrown into longitudinal folds which do not wholly disappear on stretching. Among these, four are distinguished by their larger size. The folds are somewhat irregular, dividing and uniting at acute angles in several places.

Fig. 12.— Lateral view of skull with exposure of auditory region.

1. Roof of dorsal spiracular chamber cleared of muscle and fibrous tissue.
2. Seventh nerve.
3. Spheno-maxillary fossa.
4. Infraorbital nerve.
5. Optic nerve.
6. Attachment of pterygoid muscle.
7. Rostral air sac.
8. Meckel's cartilage. (The leader should be half an inch longer).
9. Os tympanum.
10. Hyale.
11. Sigmoid process.
12. Tympano-mastoid.
13. Exterior auditory meatus.
14. Opening of lateral air sacs.
15. Zygomatic process.
16. Postorbital process of frontal.

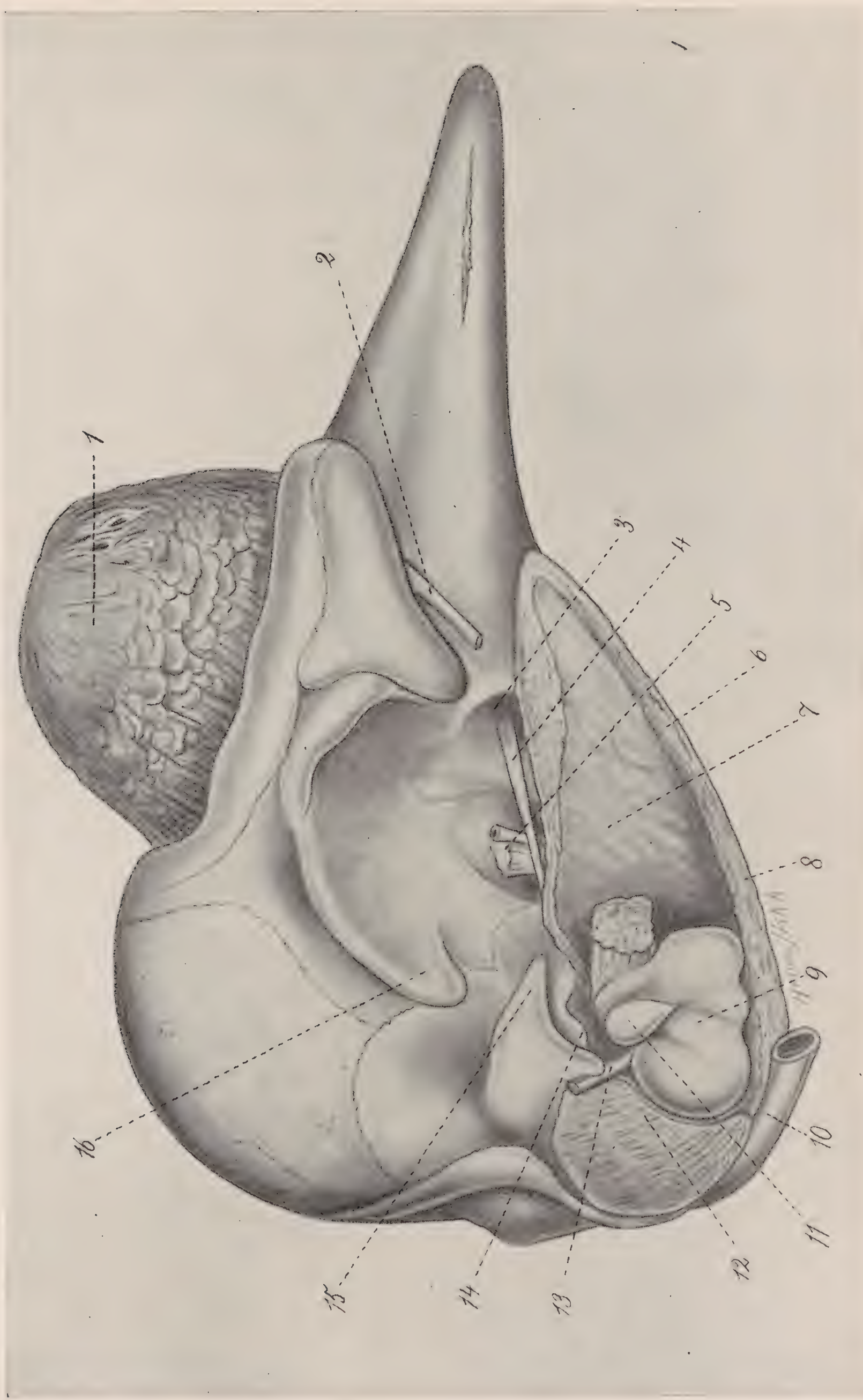


Fig. 12.

EAR

The bones related to the organ of hearing in *Kogia* have already been thoroughly treated by one of us (Schulte). No detailed description is called for here. We should like to recall one or two points concerning their position and nature, then go on to deal with the soft parts.

There is no bony canal. The os tympanum has the form of a semi-cylindrical sea-shell, with a thin irregular lateral border and a massive rolled-over mesal border. It encloses a small tympanic cavity and a larger space in the bulla ventrad thereto.

The periotic consists of the two divisions usual to the auditory apparatus of mammals: the canalicular and cochlear, the first of minute size. From

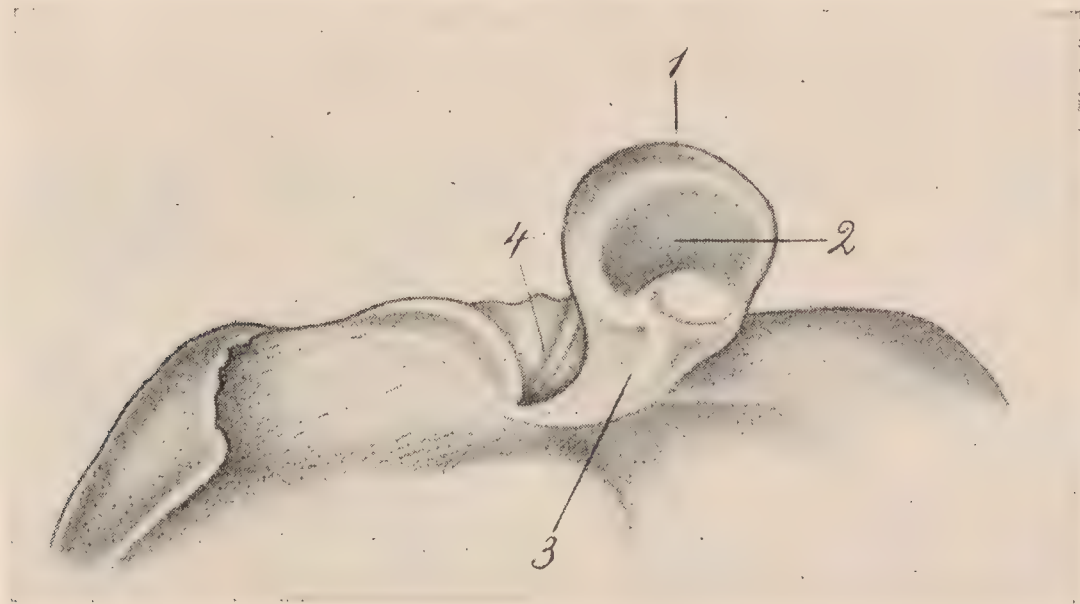


Fig. 13.—Mesal view of fragment of tympanum with malleus attached.

1. Caput mallei.
2. Articular surface for incus.
3. Processus longus.
4. Recession in border of os tympanum laterad to processus longus.

the canalicular region, a massive process extends in either direction rostrad and caudad; the first representing the tegmen tympani of other mammals, the second, the mastoid process.

These two bones are united by bony union in two comparatively small areas and are elsewhere separated by fissures of varying width. Together, they lie entirely outside the cranial cavity in a space bounded by the basi-occipital, the exoccipital, and the squamosal, and are buried in a mass of cavernous tissue enclosing blood and air spaces which will later be described.

The external auditory orifice is a minute opening situated caudad and ventrad to the eye. There is no trace of an auricle, nor can we define any distinct muscles related to the margins of the orifice. The meatus

passes mesad and slightly rostrad, in a groove of the glenoid process of the squamosal, to terminate at its attachment to the os tympanum in the notch just caudad to the sigmoid process. The walls of this canal are of firm fibrous structure, of moderate thickness, and without cartilage as far as we could ascertain. The mouth of the canal and at first its lumen are so minute as to forbid probing. Approaching the tympanum, the lumen expands in a trumpet shaped manner, though still being of an insignificant size.

The tympanic membrane is an exceedingly thin sheet, faces dorso-mesad, and is attached to the caudal and ventral borders of the notch it bridges. Rostrad, it passes beyond the border to find attachment in a groove on the ental surface of the sigmoid process in the manner described by Denker¹ for *Phocæna*. Dorsad, it is attached to the fibrous band which bridges over the space between the anterior and posterior conical processes. As far as could be ascertained, the surface of the membrane is slightly concave ectad, as in other odontocetes and in young baleen whales. It possesses the usual "triangular ligament" connecting its inner surface with the malleus.

The tympanic cavity, lying between the periotic (dorsad) and the broad rolled-over mesal border of the os tympanum (ventrad), is a comparatively limited space, owing its dorso-ventral extension chiefly to the hollowing of the tympanic surface of the periotic. It has, however, communications with extensive air spaces lying beyond the borders of the limiting bones.

The cavity, in its natural state, is occupied by a mass of thick tissue which lines its walls and nearly fills it, in this manner concealing the contents. Wherever the tympanum and the periotic fail to meet it fills in the space between them and is continuous with the mass of cavernous tissue in which the whole complex lies buried. So it, too, is undoubtedly of a cavernous nature. It fills in the hollow of the bulla and extends into the excavation beneath the inverted mesal border of that structure, also into the excavation of the tympano-mastoid. This cavernous tissue is of the greatest importance in regulating the pressure within the middle ear when the animal is submerged.

On removal of the cavernous tissue the structures of the middle ear come into view. The inner wall (or dorsal wall, as it is here) presents, caudad, a short caudo-rostrad groove bordered by prominent ridges, the channel for the seventh nerve. Mesad to the groove is a ridge which is overlain by the stapedius muscle, and, just at its termination, the stapes is firmly secured but not ankylosed in the fenestra ovalis. Rostrad to this is a

¹ Denker, A., 1902, Zur Anatomie des Gehörgangs der Cetacea, Anat. Hefte, XIX.

large depression occupying half the width of the tympanic surface of the bone. When the various parts are in their natural position this depression is occupied by the head of the malleus. Jutting underneath the orifice of the ductus fallopii is a prominent spicule, against which rests the short process of the incus. No tensor tympani was discovered though a groove for one has been noted (Schulte) in the position in which we should expect to find that muscle. It is of interest to state here that in another odontocete (*Tursiops*) a distinct tensor tympani has been found by one of us (Kernan) — a fact not hitherto noted and by some specifically denied (Denker). It is here much less defined than in the baleen whales.

The ossicles, in their general formation, do not differ from the usual mammalian type. The malleus has a proportionally large head, which lies in the depression in the periotic already described. The manubrium mallei is fused to the os tympanum along the border of a narrow cleft which, according to Denker, in *Phocæna*, contains that structure. We have found

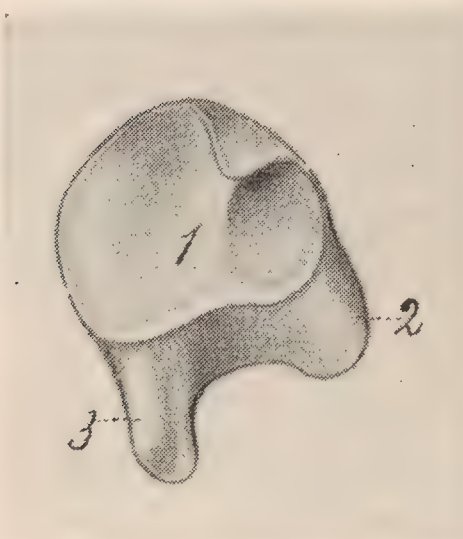


Fig. 14.

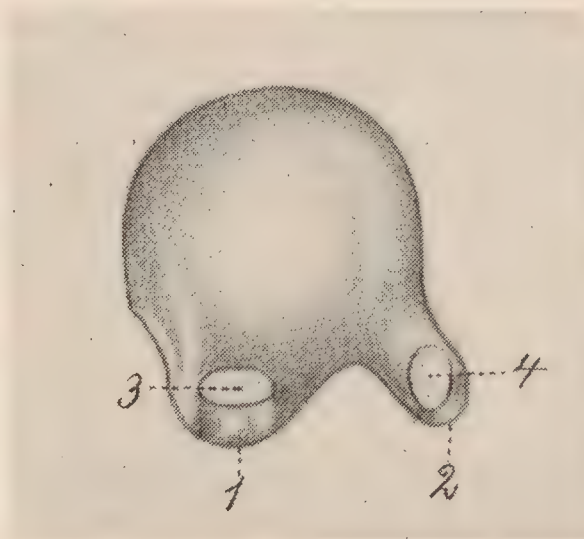


Fig. 15.

Fig. 14.— Lateral view of incus.

1. Articular surface for malleus.
2. Processus longus.
3. Processus brevis.

Fig. 15.— Mesal view of incus.

1. Processus longus.
2. Processus brevis.
3. Facette for stapes.
4. Facette for tubercle on crista facialis.

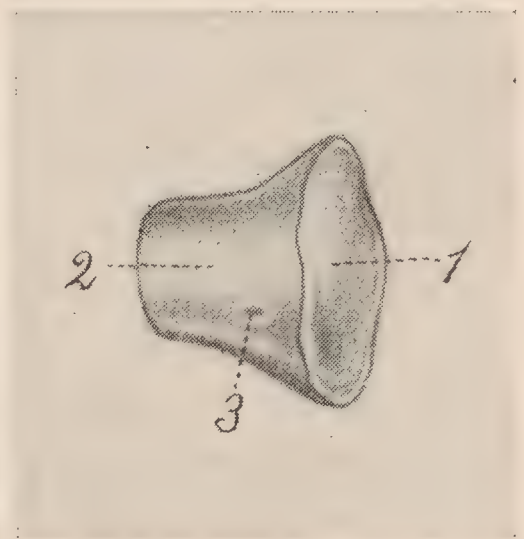


Fig. 16.

Fig. 16.— Stapes.

1. Foot plate.
2. Shaft.
3. Dimple indicating fenestra.

in *Tursiops* an arrangement like that in *Kogia*. The usual saddle-shaped articulation unites malleus and incus. The latter bone is distinguished by the fact that the two processes are of equal length, although the processus longus is the thicker. The processus brevis meets, at its tip, a small tubercle

which juts out from the crista facialis dorsad to the fenestra ovalis. The stapes is not fenestrated and sits firmly in the oval window. The non-fenestrated condition is doubtless secondary, as Denker describes small depressions in the stapes of *Phocæna* which indicate the existence of a fenestra, and we have observed the same in other of the odontocetes, namely, *Ziphius* and *Tursiops*.

The tympanic opening of the facial nerve lies just above the oval window. At this point the nerve turns sharply dorsad and takes a straight course through the periotic. Thus, the geniculate ganglion must lie in the tympanic cavity. This is due to the non-development of that portion of the tegmen tympani which in other mammals (as, for instance, man) covers in the facial canal for the latter part of its course in the tympanum. A minute canal for the great superficial nerve passes rostrad between tegmen tympani and periotic, as it has been found by us in *Tursiops* and *Balænoptera*. Owing to the fact that the periotic lies entirely without the cranial cavity, the great superficial petrosal nerve is entirely without the skull.

There are two points of contact and fusion between the os tympanum and the periotic: the anterior is, in this animal, already a bony union; the posterior consists of an exceedingly firm fibrous union of the tympanic process of the periotic to the dorsal surface of the tympano-mastoid. Except for these points, the bones are not in contact and the intervals are filled in by cavernous tissue.

At three places this tissue wall is broken and here the air space of tympanum communicates with the system of air spaces without. These have been described by Denker for *Phocæna* as lying in three groups: laterad, caudad, and rostrad. We find a like arrangement in *Kogia*. The lateral group opens out through the space between the membrana tympani and the periotic. It here consists of a few small cells. The posterior group communicates with the tympanum by an opening laterad to the facial canal and lies in the space bounded by the tympano-mastoid and the basi-occipital process of occiput. These cells also are of insignificant size. The anterior group, opening through the gutter of the os tympanum, contains only one cell but this is of remarkable dimensions. It is an oval space, 3 cm. by 5 cm., which occupies the whole of the pterygoid fossa. Its mesal wall, as are the walls of all these air sinuses, is made up of a thick pad of cavernous tissue. Its thin outer wall is overlain by the internal pterygoid muscle. Ventrally, in the angle of junction of the mesal and lateral walls, a minute opening allows a probe to pass through the pterygoid notch into the naso-pharynx. Thus, this large space is evidently an expansion of the Eustachian tube. Its communication with the naso-pharynx and the intimate relation to its lateral wall of the pterygoid muscle evidently permit of its distension by air and the expulsion of the same.

If we consider the presence of these air cells in connection with the cavernous nature of their walls, for we must remember that the whole otic complex is surrounded by a mass of cavernous tissue which fills every possible space — we will see that this region may be entirely filled with blood, the air spaces being obliterated, or, on the other hand, with air, the blood spaces being in their turn empty. The purpose of this arrangement is probably hydrostatic, making possible the submergence of the head or its sustension above the surface without effort. Again, we may think that these extensive air spaces, since their walls are trabeculated, afford additional surface for the absorption of oxygen by the blood.

The auditory apparatus of *Kogia*, as in other Cetacea, has thus been modified from an apparatus designed to receive air-borne sounds to one designed to receive water-borne sounds. The external meatus has been practically closed, the drum membrane fixed, and the ossicles rendered immovable by the fusion of the malleus to the os tympanum. Denker has thoroughly demonstrated that vibration of the ossicular chain is impossible. The water-borne sounds are evidently transmitted to the cochlear apparatus through the solid tissues of the head. This method of hearing is all the more efficient on account of the closing off of sounds borne through air, in accordance with the well-known clinical fact that bone conduction is increased where the function of the middle ear is diminished.

The manner in which the sounds are transmitted to the cochlea is disputed. Some authorities maintain that the vibrations are transmitted to the air in the tympanum, and thence to the cochlea through the fenestra ovalis. Others say that the sound waves reach the receptive organs in the cochlea directly through the walls of the periotic bone. In this connection, it is important to recall that the os tympanum and the periotic are nowhere in contact with the other bones of the skull and that they are surrounded by numerous cells capable of distension with air. So it seems necessary to suppose that sound waves must reach the internal ear through a cushion of air immediately related to the periotic, though not necessarily that contained in the tympanum alone.

The large relative size of the cochlear division of the periotic argues an active hearing function. On the other hand, the comparatively small size of the semicircular canals is what we should expect in an animal living in the water where little active balancing would be called for.

**Article IX.—THE GEOGRAPHICAL DISTRIBUTION OF COLOR
AND OF OTHER VARIABLE CHARACTERS IN THE
GENUS *JUNCO*: A NEW ASPECT OF SPECIFIC
AND SUBSPECIFIC VALUES**

BY JONATHAN DWIGHT, M. D.

PLATES XI-XIII, AND FIVE MAPS

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INTRODUCTION

Perhaps the most vexing problem that systematic ornithology presents is that of relationship. Nomenclature hinges on how we decide that one group of birds is related to another, and it has been divergence of opinion quite as much as divergence of structure and plumage that has added so greatly to our burden of scientific names. The recognition of geographical races with the use of trinomials has broadened the field of nomenclature and led many a novice to believe that the naming of a new race is the highest aim of ornithology. Furthermore, there has been a growing tendency hastily to apply names to every sort of variation, letting the facts catch up with the names as best they may — a procedure that is a good deal like putting the cart before the horse. The intensive search for differences has greatly exaggerated their importance and true perspective of values is often completely lost so that, with vision narrowed to seek only differences, nothing can be seen except a variation to be named. Ornithology is really suffering from an indigestion of names — a malady that our specialists augment rather than cure, if we may judge by the confusion that may still be found in groups of birds that have been revised by them. This is largely because the analytical side has overbalanced the synthetical, the result being that names, good and bad, accumulate.

Like many another group, the Juncos from time to time and here and there have been subjected to occasional subdivision and critical analysis and, as a consequence, we now have to deal with a mixed assemblage of names representing species, subspecies, and hybrids, concerning the status of which there is general lack of accord even among the highest authorities. Many important facts have been brought out in a very considerable literature but great diversity of opinion still prevails as to how the Juncos should be classified and named. It is not, however, as much my purpose to attempt a complete revision as it is to focus attention upon them from a new angle, for I am convinced that current explanations and conclusions are inadequate and based upon false premises. We need to break away from beaten paths and to measure or weigh variation and relationship according to new and, if possible, more stable standards. How this may perhaps be accomplished I shall presently show, for my task practically resolves itself into two parts: the marshalling of scattered facts, and the offering of explanations that seem to fit them best.

One of the great stumbling blocks in systematic work in any group of birds is usually the lack of breeding specimens, for only by means of them is it possible to learn definitely the limits of variation at different localities. However unsatisfactory their plumage may be because of its worn and often tattered condition, they are indispensable in fixing the geographical ranges of species and races and, without them, the naming of new forms is so beset with uncertainties that the literature is positively clogged with wrong and untenable names, based on winter specimens taken far from their breeding grounds. Fortunately for me, not less than five hundred breeding Juncos have passed through my hands, as well as several thousand others taken at all times of the year. The exact number is immaterial, for mere quantity means nothing unless sex, age, plumages, and localities are well represented. If we are not sure of the sex of a specimen, do not know if it is a young bird or an old one, and are, perhaps, unfamiliar with the regular plumages of the species, the folly of giving it a name because it *seems* to be different, becomes apparent; and yet this has been done time and again to the discredit of the aspirant to "a place in the sun" — and the folly is by no means confined to amateurs. My special endeavor for a number of years has been to obtain reliable specimens, and a large number collected by me have been examined when fresh, so that I can speak with some assurance upon all of these points. It is surprising how many birds wrongly sexed and without even a question mark we find in all collections. However, in spite of difficulties, the series of Juncos at my disposal has been fairly adequate and I am greatly indebted to museums and private collectors for the loan of valuable material, especially to the following: Academy of Natural Sciences, American Museum of

Natural History, Museum of Comparative Zoology, U. S. National Museum, Victoria Memorial Museum, Carnegie Museum, Mr. C. F. Batchelder, Dr. L. B. Bishop, Mr. Wm. Brewster, Mr. J. H. Fleming, and Mr. P. M. Silloway.

The colored plates to illustrate the plumages of the Juncos have been prepared by Mr. Henry Thurston and they are somewhat diagrammatic in order that comparisons may be made. These plates and the maps have been prepared under my supervision.

GEOGRAPHICAL RANGE OF THE GENUS

There are reasons why it seems desirable to consider first of all the distribution of the genus as a whole, chief emphasis being laid on the breeding range. The birds of the genus *Junco* are rather abundantly distributed in the breeding season throughout most of the forested parts of the Hudsonian and Canadian faunal zones of North America. This distribution corresponds quite closely to that of the coniferous forests of the North, especially of spruces and firs, while south in the mountains of Mexico and Guatemala the Juncos occur in the more or less isolated pine forests of the higher ranges and peaks. After a considerable gap in Central America where no Juncos have been recorded (although pine forests are found), an aberrant form occurs in the bushy zone below the cones of some of the highest volcanic peaks of Costa Rica and Panama. The breeding range of the northern birds reaches its southern limit at or near the summer isotherm of 60°, and it is possible that a like temperature governs their range on the mountains farther south. Their northward range in the Hudsonian Zone reaches tree limits in some of the wooded river valleys extending finger-like into the Arctic Zone; but from the northern limit of trees southward, approximately to the United States boundary, they range across the continent in a wide belt from the Atlantic to the Pacific, and from sea-level to timber line on the mountains. In the East they extend irregularly southward on the Appalachian Mountains wherever the conditions of the Canadian Zone prevail; and in the West a similar extension southward on the Rockies, the Sierras, and the coast ranges carries their distribution somewhat disconnectedly along the higher mountains of western Mexico to those of Central America. They breed at sea-level as far south as the Maine coast in the East, and south to northern California in the West. They reach southern California in the mountains at over 4000 feet, but southward in the Rocky Mountains of Wyoming and Colorado they remain near or above 7500 feet, and farther south in Arizona and Mexico they range from 7000

to 12,000 feet, reaching the highest altitudes in southern Mexico, Guatemala and Panama. Isolated groups are also found in the Black Hills of South Dakota (5000 to 7000 feet), in the San Pedro Martir (6000 to 10,000 feet), and the Cape San Lucas mountains (6000 to 8000 feet) of Lower California and in Guadalupe Island. The "Junco" (*Junco siemsseni*), described from China (Martens, 1906, Ornith. Monatsberichte, XIV, pp. 192-194), need not occupy us here, for it evidently has no affinities with this genus and was rightly put among the Buntings (*Emberiza*) by Dr. Sharpe (1909, Hand List, V, p. 283).

The winter distribution of the southern breeding Juncos is effected largely by altitudinal migration from the mountains down to the sheltered valleys and lowlands; but the northern birds of Canada and the United States migrate, driven by the rigors of a northern winter, entirely out of their summer habitat and are found, from October to May, over nearly all of the United States and a portion of Mexico. Their appearance in flocks among the shrubbery even before the first flakes of winter snow have fallen along the Atlantic seaboard gave rise to the name "Snow-bird," by which appellation they are still known in many localities. The slaty birds, flashing their white tail-feathers as they flit away when disturbed, are familiar objects to many of us. This outline of distribution will be filled out more in detail when we take up the different forms by name.

Could we trace the geological history of the Juncos, it would throw a flood of light on their present-day relationships, but we must content ourselves largely with surmise and conjecture. The limited migration range would seem to indicate a comparatively recent origin for them, and the fact that they form a homogeneous group, not considerably differentiated, also points this way. There are reasons, too, for supposing that the interplay of divergence and convergence may account for some of the differentiation we find today, and we may well speculate as to the significance of the almost constant association of the genus with coniferous forests; but these matters may well be left to the consideration of the palæontologist.

GEOGRAPHICAL DISTRIBUTION OF COLOR CHARACTERS

Maps 1-4

In following out my lines of investigation we are to view the Juncos from a new angle, first determining their most essential characters by analysis, then tracing the geographical distribution of these characters, and, finally, grouping the birds synthetically according to similarities rather than differences.

What then are their characters? They are of two kinds, qualitative and quantitative, which include all differences of structure, size, proportions, pattern, and coloration. In structure, the Juncos are Sparrows, and they are all practically alike; in size and proportions, their differences are quantitative; but, in pattern and coloration, the variations are both quantitative and qualitative. With one exception, the pattern of plumage is very similar, so we must turn chiefly to coloration in order to find characters or differences by which they may be separated into groups.

Color variations, therefore, give us most of the characters on which the various species and subspecies of the group are based, and they alone give us characters that may be considered wholly qualitative. No analysis would be complete if it did not take into account and weigh each factor that necessarily counts in determining rank and relationship. However, it is not my purpose to consider every demonstrable character; rather, I wish to fix attention upon the method by which it may be done. The *pattern* of plumage of most of the Juncos does not show much variation, although the *color* of certain areas of plumage varies widely at different parts of the birds' range. By mapping the geographical range of the colors of these plumage areas, it may be demonstrated that certain colors or combinations of color are peculiar to definite geographical areas. The Juncos, with colored areas of plumage sharply defined, lend themselves admirably to illustrating the principle involved in analysis of this sort, which may be extended so as to include colors of other parts than the plumage.

Basing my conclusions on the evidence afforded by breeding males, I have selected the following nine areas and parts in order to trace the geographical distribution of color in them, viz.: (1) Head; (2) Breast; (3) Back; (4) Sides; (5) Wing-coverts; (6) Tail; (7) Lores; (8) Iris; and (9) Bill.

1. *Head* (Map 1)

The area of plumage involved includes the top of the head down to the eyes and back to the nape. Three distinct types of coloration may be recognized in it; slate-gray, black, and ash-gray.

The range of the slaty heads, roughly stated, is over a large part of Alaska, Canada, New England and the higher Alleghanies; that of the black heads includes southern Alaska, British Columbia, western Washington and Oregon, and California; while the ashy heads are found south of the Canadian boundary in the Rocky Mountains and in the mountains of western Mexico and Central America as far as Panama. In these three types the color differences are qualitative and constant over definite areas



of country, although where the areas meet we find a merging or gradation from one color to the other. It may be urged that the differences between these colors, if such they may be called, are not qualitative; but my contention is that in quality they are elementally so different that one, when typical, cannot be mistaken for either of the others. It is a qualitative difference of color with black, slate, and ash as the three standards for comparison without regard to intermediate shades. How the three may have been evolved need not concern us here; we find three types of coloration today that, according to prevailing standards, call for specific names.

The mountains around the Lynn Canal in Alaska act as a snowy barrier and separate the slaty-headed from the black-headed birds, and a rather sharp transition from one to the other type takes place within a comparatively few miles. Farther south, a similar transition takes place but it is spread over a much wider area of country. Along the Canadian Pacific Railroad, for instance, we find black-headed birds as far east as Banff, Alberta, and gray-headed ones as far west as Sicamous, British Columbia, while in the region between we often find both types of head in birds nesting almost side by side. Some, too, are neither slaty nor black but show intermediate shades with, sometimes, ashy shades that suggest an intrusion of the ashy element from the south. This ashy element seems barely to touch the slaty in southeastern Alberta, but it meets the black on a considerable frontage in northern Idaho and adjacent territory. It is obvious that, if a mixture of the black and the slaty elements produces various grays, so too a mixture of the ashy and the slaty elements will also produce various grays. Consequently, it is impossible to map with accuracy the exact dividing lines between these three types of color which, unless I misread the evidence, are not merely quantitative variations but are distinctly qualitative.

The slaty type of head, however, does show slight quantitative variations in the birds of the southern Alleghanies and of the Black Hills of South Dakota; the black of the heads of birds on the coast of California near Monterey is less intense; and the ashy head is paler in the arid regions of Arizona and northern Mexico and at Cape San Lucas. The ashy head is darkest in birds from Guatemala and is obscured with a greenish or olive-brown tinge which is also found in specimens from Costa Rica and Panama. In the last group we find, in addition, faint dusky longitudinal streaking.

It is evident then that, judged by the head alone, the Juncos may be divided into three groups showing qualitative characters, these groups in turn being marked by lesser quantitative differences.



Map 2.—Distribution of color in breasts of Juncos.

2. *Breast* (Map 2)

This area of plumage is usually set off from the white abdomen by a decided line of demarkation. Four types of coloration may be made out: slate-gray, black, ash-gray, and smoky gray or dull white.

The slate-gray breast, associated with a similarly colored head, occupies the same geographical area; and the black breast and head also belong together in their distribution. The ash-gray breast, however, is associated with a similar head only as far south as Colorado for, throughout this state south to Arizona, the gray of the breast becomes paler than that of the head, while in southern Arizona and northern Mexico the gray is scarcely perceptible, the whole lower parts of Juncos from this portion of their range being of a smoky gray or dingy white. In the less arid mountains of southern Mexico and Guatemala the gray is again slightly deeper, although much paler than that of the head; while in Costa Rica and Panama it has a peculiar, slightly yellowish tinge.

While these various types of coloration merge more or less gradually at their points of contact, like the types of coloration of the head, they are sufficiently distinct qualitatively to be assigned to definite geographical areas. There are also some slight quantitative differences just as with the head.

3. *Back* (Map 3)

Four distinct types of coloration mark the back: slate-gray, brown, red, and black-streaked.

The slaty type of back is associated with a similar head and breast, and has the same distribution; the brown back is associated with all of the black-headed, black-breasted birds and with a part of those of the ash-gray type; the red back belongs wholly with the ash-gray type; and the streaked back is confined to the peculiar Juncos of the highest volcanic peaks of Costa Rica and Panama.

The slate-gray and the red types are evidently based on more stable colors than is the brown, and show very little variation either seasonal or geographical; but the brown type is susceptible to considerable variation, due apparently to climatic influences. On the Queen Charlotte Islands and the adjacent mainland where the rainfall is heavy, we find a deep and ruddy brown, while southward on the coast the brown averages slightly paler; eastward and southward to the Rocky Mountains of British Columbia and Alberta, the brown loses in depth and ruddiness, becoming more of a wood-brown at its extreme eastward extension in Idaho, Montana, and Wyoming.



Map 3.— Distribution of color in backs of Juncos.

This last type of back is also very similar to that of the isolated groups of Juncos on Guadalupe Island and in the San Pedro Martir Mountains. In California, the brown is paler than it is farther north and with a distinct pinkish instead of reddish tint, except in a damp coast belt near Monterey where the back is again dark, approaching in this respect the specimens from Alaska. Although, through wear, the brown backs of some birds may become ruddier or more rufescent in the breeding season, they never approach in color the much brighter red that is characteristic of the birds of the southern Rocky Mountains and Mexico.

With comparatively little variation, the red type of back ranges on the mountains from southern Wyoming to Guatemala. At the latter point, however, the red is diminished and much diluted or obscured by a greenish or olive-brown element, perhaps derived in the past from the Juncos to the south. These southernmost Juncos of the peaks of Costa Rica and Panama have backs quite unlike any other in adult plumage, for the color is an olive-brown with dull black streaks, resembling in this respect the juvenal plumage of the other Juncos although it seems as if this character might have been derived from an ancestor that was not a Junco. It is of interest to observe that in the birds of Mexico the red runs over into the wings extensively, while in the more northern birds of Colorado the red diminishes to a small "saddle," the scapulars being without any traces of red. In arid regions the red is a little paler and the palest red is in birds of the Cape San Lucas region of Lower California. Again, we have here at least four distinct types of qualitative coloration referable to definite geographical areas, while quantitative variations are also demonstrable between certain limits.

4. *Sides* (Map 4)

The wash of color along the sides and flanks is a very variable character that is not easily classified, but it seems possible to resolve it into five types: slate-gray, pink or vinaceous (rarely brownish), ash-gray, greenish or olive-brown, and cinnamon-pink.

The distribution of the slaty sides coincides with that of the slaty head, breast and back; the pinkish sides of varying shades and extent, with that of the brown back; the ashy sides, with that of the red back as far south as New Mexico; the olive-brown is peculiar to birds farther south; and the cinnamon tint, to those of Cape San Lucas. The last is a peculiar color that may be related to the pinkish wash but it is so unlike it that it appears to be a matter of quality rather than of quantity. It is a striking fact that the pink type not only intrudes itself between slaty and ashy types north and south of it, but it displays its maximum intensity where this finger of



Map 4.—Distribution of color in sides of Juncos.

color is thrust eastward across the Rocky Mountains. It may be that the color originated in this area and has spread westward to the Pacific Coast, where it is diminished in extent and darkened somewhat by the heavier rainfall; but it is a very stable color and varies more in quantity than it does in quality.

5. *Wing-coverts*

The upper wing-coverts, especially the greater, are usually colored much like the back, although brown-backed birds usually have gray coverts which are sometimes tinged with brown; some red-backed birds, too, have gray coverts, and white wing-bands in one small group of Juncos is also an exception. We may, therefore, classify the coverts and recognize four types: slate-gray, red, white, and olive-brown.

The slaty coverts are peculiar to all Juncos as far south as southern Arizona; the red, to those of Mexico and Guatemala; the white, to those of the Black Hills of South Dakota; and the olive-brown, to the birds of Costa Rica and Panama. While there is wide range in these variations, they are susceptible of being grouped. We do not, for example, ever find red coverts in Canada or white ones forming a wing-band anywhere else than in the Black Hills, although occasional specimens of Juncos from elsewhere may have coverts slightly tipped with white. These differences are certainly qualitative and have definite ranges, although there is no sharp line between them. Birds of the intermediate areas show intermediate characters.

6. *Tail*

The amount of white on the outer tail-feathers of the Juncos is a character that may well be considered as on the border-line between qualitative and quantitative. If weighed by its presence or absence, we must consider it as the former; and, if by its degree or extent, we must regard it as the latter. Assuming quality as the standard, we shall find only the peculiar Juncos of Costa Rica and Panama without white in the tail, and all the others with more or less of it; assuming quantity as a standard, all of the Juncos would belong in one group differing only in degree, for, although there is much individual, sexual, and geographical variation in the amount of white, it varies (geographically considered) from the involvement of three or four feathers to the vanishing point. The isolated group in Panama and Costa Rica has none, although a suggestion of white is visible if specimens are held to the light at a certain angle; in Mexico only the outer pair, on an average, is largely white; in the southern Rockies at least two pairs are white; in Montana and Idaho three pairs are white; while northward and

westward from the Canadian boundary the average is again only two white. The maximum is reached in the group of Juncos in the Black Hills, where as many as four pairs may show white. Excepting the southernmost group, all of the differences between the others are quantitative.

7. *Lores*

Like the white of the tail, the blackness of the lores is mostly a quantitative character; but it, too, may be present or absent, and it shows a great deal of variation in extent, even in birds of the same locality. It is usually absent in slaty-headed birds, although often strongly indicated; it cannot be demonstrated in the black-headed birds for obvious reasons; and it is found in all ashy-headed birds, reaching its average maximum of intensity in Mexico.

8. *Iris*

Judged according to the color of the eyes, the Juncos fall into two distinct groups: those with a brown iris and those with a yellow. All birds north of Arizona and those of northern Lower California and Guadalupe Island have brown eyes; all others have yellow ones, and the line dividing the two groups is sharp. There are, perhaps, lesser shades of color to be made out, but these two major divisions are conspicuous and the character is obviously qualitative.

9. *Bill*

Two types of coloration mark the bill: in one both mandibles are flesh-colored; in the other the upper mandible is dusky and the lower bright yellow. The first, like the brown iris, is peculiar to all birds north of Arizona and to the singular Juncos of Costa Rica and Panama; the second embraces all the other Juncos, the one found at Cape San Lucas varying in having the upper mandible brownish rather than dusky. Here again, in so slight a character as the color of the bill might seem to be, we have a difference that is qualitative beyond all question; and yet where the ranges of the two come together in Arizona there are found intermediate specimens with upper mandibles more or less dusky and the lower ones more or less flesh-colored.

This sort of analysis might be carried out to include other parts of the birds, but we have, I think, gone far enough to illustrate the possibilities of classifying them by characters that have a demonstrable geographical range. A little superimposing of such maps of color distribution will show

in a composite way how a grouping of Juncos according to color similarities may be effected. Before, however, it is possible to apply names to the groups, attention must be directed to the question of relationships because the specific or other name applied depends upon the point of view we take.

RELATIONSHIPS OF SPECIES, SUBSPECIES, AND HYBRIDS

Systematic ornithology has found it convenient to consider a species to be a group of birds, breeding true to type, that shows no intergradation with another group; a subspecies, or geographical race, as merely a variable portion of the species; and a hybrid as an individual resulting from the cross-breeding of species. The species is the unit; the subspecies is part of the unit; and the hybrid is an individual that is a part of two units. The usual hypothesis is that at one time there was but one species and that gradually differentiation of this species into the others took place. A glacial epoch, a folding of the earth's crust, environment, or some other reason is required to explain why there is now more than one of the entities we call species. Originally they have been like a chain, and if it broke into pieces or segments creating a gap or gaps in the continuity we have had new species. The links of the chain or of its segments are the subspecies. As long as the chain or the segments remain unbroken — no matter how different may be the two ends — it, or they, are species. We assume that a process of differentiation is constantly going on, and where we find several species in a group today we think of them as being remnants of a broken chain. With each remnant we have links, the subspecies or geographical races or variations within the species, and they are also called incipient species because a break in continuity may at any time elevate a segment of links, or even one of them, to full specific dignity. As long as intermediate specimens or connecting links occur — intergradation it is called — we must recognize but one species, these intergrades, no matter how great their variation, being the basis on which subspecies are founded. This rather crudely expresses current ideas regarding the derivation of species and subspecies. Nomenclaturally, we bestow a binomial upon the species, a trinomial upon the subspecies, and deem the hybrid to be such a freak that it gets no name except by mistake.

One theory is as good as another, provided it is supported by the facts; and because we have been explaining things for years in one way is no reason why another explanation may not be equally pertinent. My study of the Juncos has convinced me that some parts of our theories are inadequate and that our nomenclature in some respects is lacking in scientific accuracy.

It is not necessary to call utterly dissimilar groups races simply because we find intermediate specimens. We need only to assume either that such groups have differentiated to a point where their characters are now what we recognize as specific, or that specific characters were acquired in a geological past and that the species are now convergent and hybridizing on a large scale. In the first case we break, for convenience, the continuity of the theoretical chain today without waiting for the future dislocation that is evidently on the way; and, in the second, we assume that the break has already been accomplished long ago. It has been convenient to consider intergradation as a test of species; why may it not be more convenient to test species by qualitative characters? The question may well be asked "How can we decide that certain characters are specific?" and another equally important question is "What is the evidence of hybridization?" It seems to me that Juncos answer both these questions, if we weigh their characters qualitatively and quantitatively according to the following formulæ which indicate essential (usually plumage) differences between species, subspecies, and hybrids.

1. A *species* has one or more intrinsic characters or a combination of characters not shared by another species. The characters are qualitative.

2. A *subspecies* shares *all* the characters of its parent species in greater or less degree. The characters are quantitative and without a break in the continuity of the quantity. It connects similar extremes or may be one of them.

3. A *hybrid*, as ordinarily recognized, shows, in more or less irregular proportions, the characters or some of the characters of both of the species between which it is a cross. It connects dissimilar extremes. (The results of Mendelian experiments seem to modify this definition.)

Weighed or tested in this manner, the strikingly different groups of Juncos need no longer be lumped together as races of a single species because of specimens with intermediate characters. If such groups did not today overlap at their borders they would be unhesitatingly pronounced species. The gray-headed and the black-headed Juncos, for example, may be separated specifically on the character of grayness alone in the one and of blackness in the other. Our present theories oblige us to call these dissimilar groups one species because they freely intergrade. Is it better to blindly follow the convenient rule of thumb or to endeavor to so analyze such characters as may be found that they can be weighed and an estimate made of their relative value? We have, I believe, a valid reason for a specific name in a qualitative difference and for a subspecific name in a quantitative variation. We need only to determine which it is.

If we do not hesitate to call imperfect or "spotty" blends of plumage

hybrids, why may not more perfect blends or crosses result from the continuous action of hybridization? Until actual experiments in cross-breeding along this line have been made more extensively, we cannot settle the question positively; but, at present, it looks as if our conceptions of hybrids and of geographical races have been confused. If so, the trinomial has been applied to two quite different things: the race and the hybrid.

DIAGNOSES AND BREEDING RANGES OF THE JUNCOS

Map 5

It seems to be perfectly possible to group and name the Juncos by application of the principles just set forth, and considerable agreement with the work of earlier students will be found. I hope, now, to present facts that, even if they are not convincing, will at least lead to more careful study and exact diagnoses of species and races. Differential color variations are often very slight and difficult to put into words, but so far as possible I have followed Ridgway's "Color Standards," 1912 edition. In describing plumages it is far more difficult to find terms to express the average of many specimens than it is to describe a single specimen. I have endeavored to present a broad, as well as brief, review of the various plumages, avoiding the exceptional and omitting an unnecessary wealth of confusing details which may be found in almost every book to which we turn. No localities are included in my lists (except a few involving *hyemalis*) unless I have personally verified specimens from them. The winter ranges are not given and other matters of indirect interest are not taken up because they scarcely come within the scope of this particular study of the Juncos.

1. *Junco hyemalis*. The Slaty Juncos

a.—*Junco hyemalis hyemalis*. Slate-colored Junco

b.—*Junco hyemalis carolinensis*. Carolina Junco

Plate XI, figures 1 and 1a

A.) Differential Characters of Male.

General slatiness of head, breast, back, and sides separates *hyemalis* qualitatively from *oregonus* with black head and breast, brown back and pinkish sides, and from *mearnsi* with ashy head and breast, brown back and pinkish sides. The geographical race *carolinensis* averages slightly paler on the head and is a trifle larger, with a darker bill in fresh specimens.

B.) Breeding Range.

The Canadian and Hudsonian Zones of North America, from the Atlantic seaboard west in Canada to the Rocky Mountains and to the Yukon Valley and the Seward and Kenai Peninsulas of Alaska. The race *carolinensis* is peculiar to the Canadian Zone of the southern Alleghanies, at an elevation usually above 4000 feet. It is interesting to notice how closely the range of *hyemalis* coincides with that of the Black Spruce (*Picea marianæ*) and of the White Spruce (*Picea canadensis*), following their extension to the sheltered valleys of Arctic rivers and to timber line on snow-capped mountains.

C.) Breeding Localities.

a.) *hyemalis*.

Labrador (L'Anse au Loup, Rigolet); Newfoundland (Bay of Islands); Nova Scotia (Baddeck, Whycocomagh, Newport); New Brunswick (Hillsborough, Salisbury, Grand Manan, Point Lepreau, Bathurst); Prince Edward Island (Souris, Summerside, Tignish); Quebec (Tadousac); Ontario (Missanabe, Charlton Island, Fort George, Muskoka, Parry Sound, Bruce Co., Middlesex Co.); Maine (Fort Fairfield, Long Lake); New Hampshire (Mt. Washington, Campton Village); New York (Berlin, Haines Falls, High Peak, Overlook Mountain, Summit, Stamford); Pennsylvania (North Mountain, Gallitzin, Cresson, Altoona, McKean Co.); Michigan (Cadillac); Manitoba (Norway House); Alberta (Athabaska Landing, Grand Rapid, Ft. Chipewyan, Ft. Smith); Mackenzie (Tsalwar Lake, Tazin River, Hay River); Keewatin (Ft. Churchill); Yukon (Ft. Norman); Alaska (Lake Bennett, Caribou Crossing, Dawson, Circle City, Seldovia, Homer, Sheep Creek, Ft. Yukon, Nulato, Kowak River, Chulitna River).

b.) *carolinensis*.

Virginia (Mountain Lake); West Virginia (Davis, Cold Knob, Manning's Knob); North Carolina (Roan Mountain, Black Mountain, Craggy Mountain)

D.) Plumage.

Adult males in fresh fall or winter plumage are of several shades of dark bluish slate and neutral gray set sharply off from a rather dull white abdomen. They are slightly veiled on the breast with grayish or brownish edgings; the back, nape, crown, and scapulars usually much browner and more broadly edged, but the slaty element that prevails throughout the plumage is striking. The average bird is slightly darker on the crown than on the back, although at one extreme of a large series are uniformly slaty specimens and at the other are birds showing a faint dusky cap obscurely outlined against the grayer nape. The flanks and under tail-coverts are

usually faintly buffy. Two outer tail-feathers and part, or rarely all, of a third show white. The bill is flesh-color, sometimes dusky at the extreme tip. The iris is brown.

Young males are usually more veiled and browner than adults, especially on the back, and the white of the tail-feathers is usually less extensive, but some birds are grayer and very like adult males and again some are browner like adult females.

Adult females are, with a few exceptions, of a paler slate and much browner than any but the dullest males, the brown obscuring the back and crown still more and in most specimens there is a strong brownish or sometimes slightly pinkish wash on the sides and flanks. The tail has not more than two outer pairs of feathers white and both the outer and inner edge of the second pair is often brown.

Young females are duller and browner than adults and show a large amount of variation in the shade of slate, in the amount of brown veiling, and in the extent and tint of the brownish sides. Females can seldom be mistaken for males but some, unless carefully sexed, might easily pass for them. The size of the largest females just about equals the average dimensions of males.

Juvenal Plumage of both sexes. Above, dark grayish brown, varying in depth, with broad interrupted dusky streaks; below, dull yellowish white thickly streaked on the breast and sides with dull black. There is a great deal of variation, some specimens being darker, some lighter, some very brown, some gray, and the streaking may be broad or narrow. A large part of the yellowish and brownish shades of color is soon lost by fading. This plumage in all the species of *Junco* is worn but a short time and the remiges and rectrices are the only feathers not replaced at the post-juvenal molt in August and September. By the middle of the latter month, the first winter, an "immature" plumage has been almost completely assumed.

Breeding plumage. A limited prenuptial molt chiefly in early April renews a few of the body feathers, but wear is the chief factor in modifying the autumn plumages of both sexes, adults and young. Fading and loss of feather edgings during the winter gradually (and even by April almost completely) obliterates the brown tints in males and greatly diminishes them in females, so that birds become almost wholly slaty and look a darker, duller slate, especially on the back where there is an obscurely mottled effect partly due to the shadows of the broken edges of the overlapping feathers.

It is well to remember that some young males cannot be distinguished from adults by their plumage and some adult females cannot be told from young males, but the plumage differences outlined above obtain in the average *hyemalis* as determined chiefly by my own work in dissecting upwards

of one hundred and twenty specimens taken at all seasons of the year. The differences are only average but they are quite important if we wish to make comparison of like plumages among the other Juncos where like conditions prevail.

E.) Discussion.

In size and color *hyemalis* is remarkably uniform over a large part of North America in a wide belt extending from Alaska to the Atlantic. At the southern extremity of the Alleghanies, however, there is a true geographical race, *carolinensis*, differing a little from the parent stock but merely in degree or quantitatively, as it possesses all of its characters. It is a trifle larger and paler, and the bill is darker, while the crown is uniformly gray like the back. Occasional northern specimens of *hyemalis* scarcely differ, if at all, from *carolinensis*, but the race, although based on very small average differences, seems fairly distinguishable.

Series of *hyemalis* taken in Pennsylvania, compared with others from eastern Canada and these in turn with series from the Mackenzie River Valley and from the Kenai Peninsula of Alaska, show such slight variation in size and color that I can find no grounds on which to base another geographical race.

Westward then, approximately to the eastern slopes of the Rocky Mountains, the slaty type of *Junco* prevails and there, apparently without marked climatic change or other contributing causes, *hyemalis* rather suddenly merges into the black-headed *oregonus* west of the mountains and less obviously into the ashy-headed *mearnsi* to the south. Many confusing plumages are found on the borders where the ranges of these three different Juncos come together and, unless the three are recognized as full species with the intermediate or connecting specimens considered as hybrids, it does not seem to me that they can be adequately explained. If no intermediates or intergrades existed, there would be no question as to the validity of the three species based on their color differences. The current theory is that these three groups, because they intergrade, are now only geographical races that will be species when the intermediate links are lost. My contention is that probably either they have been separate species which are now converging and hybridizing, or that they have diverged already to a point where each has evolved one or more characters not seen in the others and therefore each may be considered as *now* specifically distinct. It is merely a question of explaining the facts as we find them and a quite different hypothesis may be equally pertinent, but each of these Juncos shows an independent combination of qualitative characters and there is just as much reason for considering the intermediate specimens hybrids as there is for assuming they

are connecting links in incipient species. A number of breeding birds and hundreds of winter specimens have passed through my hands, and many of them tend to bear out my hypothesis, some at least having all the ear-marks of hybrids. It cannot be denied that the majority of intermediate specimens are what we usually call "intergrades" with a regular blending of color and that they lack the irregular mixing of characters or spottiness that we associate with hybrids, but there are some that do show just such irregularities.

A number of specimens taken chiefly in winter in the West have a curious black mottling or spotting on the back, usually associated with a more or less distinct black cap and with the slate color of the rest of the plumage verging towards black; the backs range from gray to deep brown and the sides are slaty. While we may consider these birds as being merely melanistic (because similar breeding specimens occasionally occur in the East), they strongly suggest a strain derived from the black-headed *oregonus*. The next step towards *oregonus* is shown by specimens with faintly pinkish instead of slaty sides, such birds having slaty or slightly brown-tinged backs in contrast to a nearly black head. Pinkish sides is a character peculiar to *oregonus* and it is not found in males of *hyemalis*. I have examined breeding males of these intermediate types taken at the White Pass in Alaska where the change from *hyemalis* to *oregonus* is effected in a short distance, at Brazeau Lake and other places near the Yellowhead Pass in Alberta, and at several places between Banff in Alberta and Sicamous in British Columbia where the belt of intergradation is widest. The *mearnsi* strain from the south may also account in part for the gray-headed birds that are found breeding side by side with black-headed ones at many localities along the Canadian Pacific Railway, all of them having more or less pinkish sides. The variation in females of the three species complicates the question still more, for the average females of the three differ much less from one another than do the males, and the hybrids between them would seem therefore to be much more numerous. Further discussion of this important matter will be found under the sections dealing with *Junco oregonus* and *Junco mearnsi*.

This is perhaps an appropriate place to discuss briefly and to dispose of the "*Junco hyemalis connectens*" of Coues. The original description (1884, Key North Amer. Birds, 2d ed., p. 378) is a curious mixture of fact and fancy but, fortunately, the type is extant in the collection of Mr. Wm. Brewster (No. 7046, ♀, April 26, 1882, Colorado Springs, Colo.). I have examined it and, as correctly stated by Mr. Ridgway (1901, Birds North and Middle Amer., Pt. 1, p. 276, footnote), it is clearly a specimen of *hyemalis*, and shows the characters common to sex and season. The name "*connectens*" therefore becomes a synonym of *hyemalis* and is not available,

although in the A. O. U. Check-List, 3d ed., 1910, it is revived and applied to "Shufeldt's Junco" which is quite a different bird, as will presently be shown.

2. *Junco aikeni*. The White-winged Junco

A.) Differential Characters of Male.

White wing-bands distinguish this Junco qualitatively from all the others. Except for this character it closely resembles *hyemalis*, although averaging larger, being of a paler slate, and with more white in the tail.

B. and C.) Breeding Range and Localities.

The Black Hills of South Dakota and the mountains adjacent in Wyoming.

D.) Plumage.

Adult males in fresh fall or winter plumage resemble *hyemalis*, but average paler, are uniformly gray above, and have the best part of four outer pairs of tail-feathers white. The wing-bands are usually broad and conspicuous but vary in extent.

Young males are usually slightly more veiled with brown than adults, and with less white in the wing-bands and tail.

Adult females are a little duller and paler than males, the wing-bands less extensive, and tail-feathers with the white reduced to about three of the outer pairs.

Young females are duller and browner than the adults.

Juvenal plumage is not appreciably different from *hyemalis*, except for the wing-bands and the white in the tail.

Breeding plumage. The gray loses the veiling and becomes a little dingy with wear, the prenuptial molt being slight.

E.) Discussion.

Virtually isolated as to its breeding range, its affinities, however, seem to lie with *hyemalis*, although it is geographically nearer to *mearnsi*. It shows the qualitative character of white wing-bands which is, according to my standard, specific. Only very occasional specimens of other Juncos show slight white edgings on the wing-coverts, which rarely amount to a band. It is much the largest of the Juncos and has the most white in the tail, but size and extent of white are merely quantitative characters and not specifically diagnostic. The young of this species was erroneously described as new under the name "*Junco hyemalis danbyi*" (Coues, 1895, Nidologist, III, October, p. 14), but later correction of the error was made (Coues, 1897, Auk, XIV, pp. 94-95).

3. *Junco oregonus*. The Black-headed Juncos

- a.—*Junco oregonus oregonus*. Oregon Junco
- b.—*Junco oregonus thurberi*. Thurber's Junco
- c.—*Junco oregonus couesi*. Coues's Junco
- d.—*Junco oregonus pinosus*. Point Pinos Junco

Plate XI, figures 2 and 2a; and Plate XIII

A.) Differential Characters of Male.

A black head and breast distinguishes this species from all the other Juncos. The geographical races may be recognized chiefly by the color of the back which in *oregonus* and *pinosus* is a deep ruddy brown, in *thurberi* paler and pinkish, and in *couesi* a plain dark brown.

Neither the name "*connectens*" nor "*shufeldti*" is applicable to the brown-backed bird and I therefore propose to name it in honor of the late Dr. Elliott Coues, choosing for the type a breeding male from southern British Columbia.

Junco oregonus couesi, new subspecies (Plate XIII, figs. 1 and 2)

Type: No. 16969, collection of J. Dwight; ♂; May 14, 1906; Okanagan, British Columbia. Collected by Allan Brooks.

Whole head and breast black; the back mummy-brown; the sides and flanks washed with light vinaceous-cinnamon; the rump deep neutral gray; lower parts, except breast and sides, white; the two outer pairs of tail-feathers and a dash on the third are white; bill and feet flesh-color; iris brown.

Measurements.—Wing, 79 mm.; tail 70 mm.; tarsus, 21 mm.; toe with claw, 21 mm.; culmen, 11 mm.; depth of bill at base, 6 mm.

On examination, the type of *oregonus* (U. S. Nat. Mus., No. 1949; ♂; October 5, 1834; Columbia River), a fall bird, proves to be ruddier and darker than average specimens of this race, of which we know the exact breeding range. Some of them are as deeply colored as the type but the average breeding bird of the Queen Charlotte Islands and the adjacent parts of the coast, where heavy rainfall occurs, is somewhat paler than these very dark ones. An examination of the type of "*shufeldti*" (U. S. Nat. Mus., No. 106035; ♂; October 13, 1885; Fort Wingate, New Mexico) develops the fact that this type specimen is evidently one of the slightly paler birds, apparently an *oregonus* that has wandered far south in migration. There are both light and dark ruddy-backed specimens mingled with brown-backed birds to be found in winter at many equally southern localities.

The lightest specimens are referable to *thurberi*, but in many cases it is difficult to decide whether the specimen in hand is *oregonus*, *thurberi*, or *couesi*. The brown birds doubtless originate, for the most part, inland and are the ones that I have named *couesi* because, with "*connectens*" a synonym of *hyemalis* and "*shufeldti*" a synonym of *oregonus*, there remains no old name which is applicable.

B.) Breeding Range.

Southern Alaska and British Columbia west of the Rocky Mountains, western Washington and Oregon, and the mountains of California. True *oregonus* is restricted to the islands and coastal strip of southern Alaska and western British Columbia; *thurberi* ranges chiefly over northern California and western Oregon; *couesi* extends from the western part of Washington and British Columbia to the Rocky Mountains; and *pinosus* is very local and confined to the coast region north and south of Monterey Bay, California.

C.) Breeding Localities.

a.) *oregonus*.

Alaska (Yakutat, Gustavus Point, Haines, Douglas Island, Sitka, Wrangell); British Columbia (Queen Charlotte Islands).

b.) *thurberi*.

Washington (Upper Quinault); Oregon (Elgin, Maury Mts., Paulina Lake, Tillamook); California (Ft. Jones, Siskiyou, Caleta, Sherwood, Sisson, Snow Mountain, Placerville, Fyffe, Echo, Blue Cañon, Donner, Mount Wilson, Witch Creek, Cuyamaca, San Jacinto Mountains, Smith Mountain, Laguna Mountains).

c.) *pinosus*.

California (Monterey, Santa Cruz).

d.) *couesi*.

Alaska (White Pass City, Glacier); British Columbia (Cowichan, Victoria, Wellington, Goldstream, Shawinigan Lake, Lund, Howe Sound, New Westminster, Mt. Lehman, Chilliwack, Agassiz, Spence's Bridge, Lilloet, McGillivray Creek, Ashcroft, Sicamous, Okanagan, Midway, Trail, Lower Arrow Lake, Revelstoke, Glacier); Alberta (Banff, Little Red Deer, Jasper House, Henry House, Brazeau Lake); Washington (Lummi Island, Seattle, Tenino, Mt. Ranier, Mt. St. Helens); Oregon (Forest Grove).

D.) Plumage.

Adult males in fresh fall or winter plumage have the black areas of head and throat slightly veiled (more broadly on the crown and nape) with pale brownish or grayish edgings, and the browns of the back are slightly modi-

fied with paler edgings. The amount and depth of color in the vinaceous or pinkish sides is variable and it is sometimes brown in deeply colored birds. The bill is flesh-color. The iris is brown. Two outer tail-feathers and rarely a touch on the third are white in *oregonus* and *pinosus*; more of the third is white in *thurberi* and *couesi*. The breast of *pinosus* is usually paler than the head and averages a shade grayer than the deep black of *thurberi*, and in size *pinosus* is smaller except the bill.

Young males are rather more heavily veiled and the black of the average specimen is apparently a trifle duller than that of the adult. There is usually less white in the tail.

Adult females show unusually great variation; some are like young males but they average a much duller black and are much browner, with less white in the tail. In about forty per cent the head and throat are both dull black (some identical with males); in another fifty per cent the *throat only* is dull black, the head being more or less gray mixed with black streaking or mottling; while in perhaps a scant ten per cent both the head and the throat are chiefly a slaty gray.

Young females are the dullest plumaged birds as a rule, but they show the greatest variation and the widest extremes.

Juvenal plumage. Above, similar to *hyemalis* but with a ruddy, pinkish or brownish back; *oregonus* and *couesi* are darkest below, and sometimes not distinguishable from *hyemalis*, but usually with a decided pinkish wash on the sides. The variation is very considerable even in the same brood.

Breeding plumage. A limited prenuptial molt is insignificant in its effect. Wear removes from the autumn dress most of the veilings and edgings, the black appearing to become blacker, although fading may give it a somewhat brownish tinge. The brown of the back may fade or, if it has a ruddy or pinkish tinge, it actually becomes brighter or rufescent through loss of feather edgings. The pinkish tints of the sides are more stable and not subject to much fading.

E.) Discussion.

Some two hundred and fifty breeding specimens of this species have passed through my hands, no less than one hundred of them being males from a single locality, El Dorado County, California. A careful examination of the California series is most instructive. Seventy-five to eighty per cent of these birds have the pale, pinkish brown back of *thurberi*; about fifteen per cent have browner backs, some being identical with *couesi*; and a small percentage have deeply ruddy backs indistinguishable from the paler specimens of *oregonus*; a few also have backs almost gray and with only a slight tinge of brown almost identical with the intermediates or

hybrids, as I consider them, between *oregonus* and *hyemalis* such as are found chiefly on the eastern slopes of the Rockies. These plumage variations at one locality show that breeding birds referable to no less than three recognized races occur at the same place, although only a very small percentage of them are other than *thurberi*. The aberrant percentage is made up of birds that are merely average, or more often under average, *oregonus* and *couesi*. It must be remembered, however, that we are dealing with very small differences of size and color in these races and only when specimens are laid out in series do the average differences become really obvious, except with the most typical examples. With races so finely discriminated that possibly only eighty per cent of the breeding males from the most typical localities and a smaller percentage of the females are definitely recognizable, it is easy to realize that the naming of winter specimens taken perhaps far from their breeding range involves careful matching and measuring of skins and, in a good many doubtful cases, merely clever guessing at the name most applicable.

And here the question naturally arises whether the name we are using applies to the bird or to the locality. If to the latter, we must, in the present instance, call ruddy-backed and pinkish-backed and brown-backed birds by one name, because they all occur in the same locality; if to the former, we may recognize three races by name, with the understanding that breeding specimens of any one or two of them may occur occasionally well within the limits of the breeding range of the other. The fact stands out that several different degrees of the *oregonus* plumage are found in one and the same locality; this is true at more than one point of its range. At the same time, the *average* variation may be named and restricted to a fairly definite range, so that winter specimens may be named with some assurance that the characters they show indicate their probable origin within this range, although there is no certainty of this. We can name a bird according to its plumage, but in the winter we can never be quite sure where its summer residence was, although the stronger its subspecific characters the stronger the probability that we are guessing right. The finer the distinctions of races, the less the chances of guessing right; but, if we do not name a bird from its plumage, what is there to name? It seems to me we are not naming a locality but the variations of plumage; otherwise, a name becomes a needless synonym of the name of a place. I do not see how we can escape the necessity of calling a specimen *oregonus* or *thurberi*, or any other name, if it shows the characters of the form, no matter where it is taken. We must name a bird by the plumage it is wearing not by the one that it ought to be wearing because it has been captured within the bounds assigned to another geographical race.

Another important question which arises is How shall hybrids be named, if at all? As indicated when discussing *hyemalis*, the meeting of this species and *oregonus* gives us two types of hybrids and the meeting of *mearnsi* and *oregonus* gives a third. The third was described long ago as a new species, "*Junco montanus*" (Ridgway, 1898, Auk, XV, October, p. 321), but it may be considered as either *mearnsi* darkened with the *oregonus* strain, or *oregonus* grayed with the *mearnsi* strain, as you please. In the same way, east of the Rocky Mountains we have a *hyemalis* darkened or blackened by the *oregonus* strain that, for convenience, might be called "*cismontanus*," while chiefly west of them we find an *oregonus* with the gray back of *hyemalis* that might be called "*transmontanus*." If these names could be restricted to definite geographical areas there would be some grounds for admitting the existence of three races but, as a matter of fact, breeding birds bearing these characters turn up at many localities. Birds of the "*montanus*" type occur far north in the Mackenzie Valley and west to the Frazar Valley; those of the "*cismontanus*" type occasionally appear as far east as Quebec; and those of the "*transmontanus*" type reach the Cascade Mountains, in Washington and Oregon, especially at the higher elevations which seem to have a "graying" influence. It will be observed, however, that these three types of plumage are not merely variations in color from *mearnsi*, *hyemalis*, or *oregonus*, but blends of their color characters. The birds are intermediates or intergrades between dissimilar extremes — extremes that are well deserving of specific rank, because their color characters are intrinsic or qualitative. Instead of naming the hybrids, it is probably simpler to follow the old-fashioned method of using an $\times$ to indicate them. If a specimen is nearest to *hyemalis* we would write *Junco hyemalis* $\times$ *oregonus*, or if to *oregonus*, the name should be written *Junco oregonus* $\times$ *hyemalis*, etc.

The brown of the back of *oregonus* is evidently sensitive to climatic influences, but it persists in some birds of the Rocky Mountains that breed with those of the "*transmontanus*" type. This fact alone provides a good reason, on the one hand, for considering *couesi* as a race of *oregonus* and, on the other, for considering "*transmontanus*" as the result of hybridization between *hyemalis* and *oregonus*. The line of cleavage between the species and their differentiation may, perhaps, stand in direct relation to the ice sheet of the last glacial period rather than to the Rocky Mountains themselves which, after all, form today a very weak barrier to the distribution of these hardy Sparrows.

4. **Junco mearnsi.** The Pink-sided Juncos

- a.— *Junco mearnsi mearnsi*. Pink-sided Junco
- b.— *Junco mearnsi insularis*. Guadalupe Junco
- c.— *Junco mearnsi townsendi*. Townsend's Junco

Plate XI, figures 3 and 3a

A.) Differential Characters of Males.

The ashy head and breast, brown back, and sides heavily washed with a deep buff-pink separate it specifically from *hyemalis* to the north; the ashy head and breast separate it from *oregonus* to the west; and the brown back and pinkish sides separate it from the Juncos to the south. The race *insularis* differs only in degree, being slightly darker (especially the brown of the back), slightly smaller, and with a somewhat larger bill. The race *townsendi* also differs only in degree, although the head and throat are about as dark a slate as the paler specimens of *hyemalis*, but it has a pinkish wash on the sides and the back faintly brown.

B.) Breeding Range.

Southern Alberta, western Montana and Wyoming, and northern and eastern Idaho chiefly in the mountains. The race *insularis* is isolated in Guadalupe Island, and the race *townsendi* in the San Pedro Martir Mountains of northern Lower California.

C.) Breeding Localities.

a.) *mearnsi*.

Saskatchewan (Cypress Hills); Alberta (Banff); Montana (Belt River Cañon, Big Snowy Mountains, Mystic Lake, St. Mary's Lake, Flathead Lake, Columbia Falls, Thompson Pass, Tobacco Plains); Idaho (Salmon River Mountains, Coeur d'Alene, Stanley Lake); Wyoming (Yellowstone National Park, Big Horn Mountains); Utah (Rich County).

b.) *insularis*.

Guadalupe Island.

c.) *townsendi*.

Lower California (San Pedro Martir Mountains).

D.) Plumage.

Adult males in fresh fall or winter plumage have the head and throat of a rather dark, neutral gray; and the lores black, faintly veiled with grayish or pale brownish edgings; the back is a pale mummy or sepia-brown with slightly paler edgings; the sides and flanks have a broad conspicuous wash of a buffy or vinaceous pink, varying in depth of color. A large part of the

three outer pairs of tail-feathers is white. The bill is flesh-color. The iris is brown.

Young males are usually more veiled with brown on the crown, nape, and back, and often with less white in the tail-feathers.

Adult females average a trifle paler than the males; are more veiled with brown; and have less white in the tail-feathers, the third pair seldom having even a white dash.

Young females are regularly the dullest specimens, with colors less developed.

Juvenal plumage. Above, very like *oregonus* but paler; below, the pinkish wash is more marked in average specimens than it is in *oregonus*, but at this stage birds of the two species are not very different.

Breeding plumage. A slight renewal of feathers by a limited prenuptial molt takes place, but wear is the chief factor in modifying the winter dress. The gray tints become a trifle browner or dingier, the brown of the back fades and so does the pink of the sides to a small extent. Occasionally the back is slightly reddened by loss of feather edging.

E.) Discussion.

This *Junco* occupies a considerable geographical area between dissimilar Juncos to the north and to the south. None to the south has pinkish sides and none to the north has ash-gray head and breast. Therefore *Junco mearnsi* has a combination of color characters not shared by any of the others and, according to our proposed standards, it may be considered a species. It combines, rather than connects, dissimilar extremes or there would be reason for considering it a hybrid. An argument against hybridization, however, lies in the fact that the species breeds true throughout its range and only breaks off into hybrids at the points of contact with other species.

The occurrence of Juncos on Guadalupe Island that only vary a little in size and color from typical *mearnsi*, and of Juncos in the San Pedro Martir Mountains that are very close to the so-called "*montanus*" is most suggestive of a wider distribution of the species at an earlier geological time. A shrinkage of the area seems to have left these two "oases" which are now cut off from the parent stock with dissimilar Juncos for their nearest neighbors, but that *insularis* and *townsendi* are anything else than geographical races of *mearnsi* there seems to be little doubt.

My reasons for believing "*Junco montanus*" to be the hybrid between *mearnsi* and *oregonus* have been given already, the chief one being that the hybrid shows evidence either of a darkening of the ashy areas of *mearnsi* through the black element in *oregonus* or a lightening of the black of *oregonus*

with an infusion of the slaty element in *hyemalis*. Another possibility is the darkening of *mearnsi* with the slaty element of *hyemalis* or the lightening of *hyemalis* with the ashy of *mearnsi*, although the ranges of these two species barely touch if at all. There is apparently no climatic cause for this darkening of *mearnsi* or we might have reason for considering "*montanus*" as a geographical race but, on account of its irregular characters and its somewhat sporadic occurrence over a wide area in Alberta, British Columbia, and Montana where it is often found breeding on the same hillside with *Junco oregonus couesi*, or east of the Rockies breeding with *Junco hyemalis hyemalis*, it would seem to be nothing more than a hybrid.

As we have the hybrid "*montanus*" to the north so, too, we have another hybrid to the south where dissimilar extremes, *mearnsi* and *caniceps*, meet and blend. This bird, named "*Junco annectens*" originally (Baird, 1870, Cooper Ornith. California, p. 564) and later independently described as "*Junco ridgwayi*" (Mearns, 1890, Auk, VII, July, p. 243), has the pink sides of *mearnsi* combined with the red back of *caniceps*. Perhaps because of isolation on the mountains, there is but a small area of contact between the species (in southwestern Wyoming) so that "*annectens*" is not a frequent type of plumage. I have examined about a dozen birds, including breeding specimens from Fort Bridger, Wyoming, and Arc Dome, Nevada, besides winter birds, all of them with more or less pinkish sides and with more or less red on the back, in some the red extending faintly to the wing-coverts.

In my opinion Ridgway, (1901, Birds of North and Middle Am., Pt. 1, p. 276) rightly considers all such specimens as hybrids and the A. O. U. Check-List (1910 ed., p. 268) is wrong in recognizing them as "*Junco hyemalis annectens*." In rectifying Baird's mistake in describing a hybrid ("*annectens*") it was necessary for Ridgway to name *mearnsi* (1897, Auk, XIV, p. 94).

5. *Junco caniceps*. The Gray-headed Junco

Plate XI, figures 4 and 4a

A.) Differential Characters of Male.

A red back and ashy sides separate it from *mearnsi* on the north and the ashy breast, sides, scapulars, and wing-coverts separate it from the *phænotus* group on the south.

B.) Breeding Range.

Western Colorado, southern Wyoming, northern New Mexico and parts of Utah and Nevada, being found on the mountains at above 7000 to 8000 feet.

C.) Breeding Localities.

Wyoming (Ft. Bridger, Laramie Mts.); Colorado (Dillon, Mt. Ptarmigan, Fremont Co., Estes Park, New Castle, Ft. Meeker, Mill City); New Mexico (Amizett, Willis, Twining); Utah (Uintah Mts.); Nevada (Ruby Mts.).

D.) Plumage.

Adult males in fresh fall or winter plumage have an ashy or cinereous head and breast (the latter paler), slightly veiled with grayish or pale brownish edgings, and a rather bright mahogany-red back, veiled with greenish or yellowish edgings. The sides are ashy. The lores are black. Red, like the back, sometimes edges the crown feathers. The bill is flesh-color. The iris is brown. The tail-feathers average less white on the third pair than in *mearnsi*.

Young males are a trifle more veiled on an average.

Adult females average slightly paler, especially on the crown and nape, and are more veiled, although the sexes are often alike.

Young females are duller and more veiled.

Juvenal plumage. Above, the back is dull red with dusky streaks; the head gray with narrower streaks. Below, dull white, grayer on the breast and streaked with dull black. Birds resemble *oregonus* but have a redder back even at this stage.

Breeding plumage. The red of the back through wear becomes brighter and paler (a burnt sienna or even paler) and the gray dingier.

E.) Discussion.

While the red back indicates a distinct affinity with the Juncos to the south, the ones immediately to the north have pink sides which seems to indicate that *caniceps* has no direct relationship with them. Its ashy sides are much paler than those of *hyemalis*, from which species they may perhaps have been derived. It is a sort of an intermediate or connecting link between the northern and southern groups, but its characters are so combined that we may consider them as specific. It breeds true over a definite geographical area and only at its northern and southern borders is there evidence of hybridization with the adjacent species.

We have a hybrid in "*Junco annectens*" connecting *caniceps* with *mearnsi* to the north, and another hybrid in "*Junco dorsalis*" (Henry, 1858, Proc. Acad. Nat. Sci. Phila., X, May, p. 117) connecting it with *phæonotus* to the south.

The areas of contact which we may suppose once existed between *caniceps* and *phæonotus* are now largely obliterated because of mountain isola-

tion. The hybrid "*dorsalis*" is perhaps a reminder of former conditions and, except for the bill, it shows strong affinities, even to the brown eye, with *caniceps*. The bill is about the same size as that of *caniceps* but the *phæonotus* element has blackened the maxilla and diluted the gray of the breast to a paler shade. It is the association of dissimilar characters in series of birds with irregularities in the characters that points to its being a hybrid. The variation is not of the sort that marks the geographical race nor have the characters become established to such an extent that they can be considered specific.

The hybrid "*dorsalis*" occurs at points between the ranges of *caniceps* and *phæonotus* on the higher mountains (at over 7000 feet) of Arizona and New Mexico, and specimens examined show a good deal of variation in plumage, some most resembling one species and some the other.

6. *Junco phæonotus*. The Red-backed Juncos

a.—*Junco phæonotus phæonotus*. Mexican Junco

b.—*Junco phæonotus palliatus*. Arizona Junco

Plate XII, figures 1 and 1a

A.) Differential Characters of Male.

A black upper and a yellow lower mandible, a yellow iris, and smoky or dull white underparts separate this species from all the northern Juncos, including *caniceps* which alone shares the red back. The race *palliatus* differs only in degree and not in quality from the parent stock, being merely a paler desert form.

B.) Breeding Range.

The pine forest regions of Mexico and of southern Arizona and New Mexico: *phæonotus* at about 8000 to 14,000 feet in the less arid mountains of southern Mexico: *palliatus* at about 7000 to 8000 feet in northern Mexico and the adjacent parts of the United States.

C.) Breeding Localities.

a.) *phæonotus*.

Mexico: Vera Cruz (Las Vigas, 8000 ft.), Hidalgo (Real del Monte), San Luis Potosi (Sierra de San Luis Potosi, 9000 ft.), Jalisco (San Sebastian, Volcan de Nieve, Colima, 10,000 to 14,000 ft.), Michoacan (Patzcuaro), Zacatecas (Sierra Valparaiso).

b.) *palliatus*.

Arizona (Mt. Graham, Chiricahua Mts., Santa Catalina Mts., Santa

Rita Mts., Huachuca Mts.). Mexico: Sonora (San José Mountain), Chihuahua (Pinos Altos, Pacheco), Durango (Arroyo del Buey).

D.) Plumage.

Adults of both sexes are practically alike in plumage, although some females are duller. In fresh fall or winter dress the head is an ashy or neutral gray and very much darker than the breast, which shows scarcely any line of demarkation as its very faint, smoky gray merges into the dull white of the abdomen. The back is a mahogany-red, more or less veiled with a greenish gray, which extends to the greater coverts and tertiaries. The head is somewhat veiled with pale brownish edgings, and occasional specimens have a few red edgings. The outer tail-feathers and part of the next pair are white with brown outer edges. There is a brownish wash on the flanks, diminished in extent, paler, and somewhat grayer in *palliatus*.

Juvenal plumage. This is much like *caniceps*, but paler below and without the darker gray of the breast.

Breeding plumage. A limited prenuptial molt and wear result in a bird that is a dingier smoky gray or brownish white below, with the red back much brighter and somewhat paler through loss of the feather edgings.

E.) Discussion.

This species was originally described as "*Fringilla cinerea*" (Swainson, 1827, Philos. Mag., new ser., I, p. 435) and *palliatus* was described as "*Junco cinereus palliatus*" (Ridgway, 1885, Auk, II, Oct., p. 364). The name *phæonotus* was first used by Wagler (1831, Isis, p. 526), and revived by Ridgway (1895, Auk, XII, p. 391), *cinereus* being preoccupied.

The colors of the bill and of the iris furnish characters that set apart this group of Juncos, which shows little variation throughout its range from near the United States boundary to the Isthmus of Tehuantepec.

The bright red back, yellow (sometimes almost white) eyes, and black and yellow bill are characters that obtain over an extensive north and south range. The Little Colorado River in Arizona seems to mark the northern limits of the species, but even south of this the influence of the northern Juncos is felt where we find the hybrid "*dorsalis*" (discussed already under *caniceps* the species it most resembles).

At the southern limits of the range of *phæonotus* the Isthmus of Tehuantepec causes a considerable gap in the continuity of the Juncos and, if a connecting link ever existed between this species and the next to the south, it has been lost. The same thing is true of the group of Juncos at the tip of Lower California, which shows a strong affinity with *phæonotus*.

7. **Junco bairdi.** Baird's Junco

Plate XII, figures 2 and 2a

A.) Differential Characters of Male.

The sides and flanks are broadly washed with a pinkish cinnamon color that is unlike that of any other Junco.

B. and C.) Breeding Range and Localities.

The mountains (Sierra de la Victoria, 6000 to 8000 feet) at the southern extremity of Lower California, where it is isolated and resident.

D.) Plumage.

In *fresh fall or winter plumage*, the sexes are alike and resemble very pale or faded-out *phænotus*, except for the cinnamon-pink wash of the sides. The back and wing-coverts are redder than the sides. The white of the tail-feathers is much like *phænotus*. The upper mandible is dark brown instead of black.

The *juvenal plumage* is much like that of *phænotus*, but the cinnamon tint of the sides is marked.

Breeding plumage. Similar to the winter, but faded.

E.) Discussion.

This Junco, with its red back, shows an ancestral affinity with the red-backed birds of the adjacent mainland, but the cinnamon wash on the sides is diagnostic and may be considered as specific. It was described by Ridgway (1883, Proc. U. S. Nat. Mus., VI, p. 155) and is the palest of the Juncos.

8. **Junco alticola.** The Guatemala Juncoa.—*Junco alticola alticola.* Guatemala Juncob.—*Junco alticola fulvescens.* Chiapas Junco

Plate XII, figures 3 and 3a

A.) Differential Characters of Male.

A greenish or olive-brown element suffuses the indistinctly reddish back and darkens the flanks. Otherwise, we find merely quantitative characters which connect this Junco with *phænotus* in color, in dimensions, and in diminution of white on the tail-feathers. The race *fulvescens* is a little paler and smaller.

B.) Breeding Range.

The pine forests on the high volcanic peaks of Guatemala, the race *fulvescens* occupying a somewhat similar region adjacent in Mexico.

C.) Breeding Localities.

a.) *alticola*.

Guatemala (Volcan de Fuego, 10,200 to 12,000 ft.), Quezaltenango, El Rincon, San Marcos).

b.) *fulvescens*.

Mexico (San Cristobal, Chiapas).

D) Plumage.

In fresh fall or winter plumage the sexes are practically alike, although some females are duller. The head is rather deep neutral gray; the lores are black in contrast. The breast is much paler, hardly set off at all from the still paler abdomen. The back is a dull, indistinct mahogany-red, suffused with a greenish or olive-brown tint. The sides have a deep greenish or pale olive-brown wash. The bill is very large, the upper mandible black, the lower yellow. The iris is orange-yellow. The outer pair of tail-feathers only is partly white.

Breeding plumage. Generally paler through wear.

E.) Discussion.

This Junco, described by Salvin (1863, Proc. Zool. Soc. London, p. 189), is isolated on the high mountains but the red back, derived doubtless from the north, and the greenish tint, perhaps from the south, point to a closer relationship in the past with adjacent forms. The race *fulvescens* was described as a full species (Nelson, 1897, Auk, XIV, p. 61) but it seems to be a variation towards *phæonotus*, although a wide gap occurs between their ranges where lowlands present conditions today (whatever may have prevailed in the past) that preclude the existence of Juncos.

9. **Junco vulcani.** The Volcano Junco

Plate XII, figures 4 and 4a

A.) Differential Characters.

A back with black streaks sets this Junco apart from all the others, nor does it fit into the genus in other particulars, although it seems more nearly related to *Junco* than to any other group of Sparrows. There is no white in the tail although there is a suggestion of it if a specimen be held in a certain way to the light. The feet and bill are large, the latter being flesh-colored unlike its nearest ally, and similar to that of the Juncos of the United States.

B. and C.) Breeding Range and Localities.

In bushy areas above 10,000 feet and below the cones of some of the highest volcanoes of Costa Rica (Irazú and probably Turrialba and Poas) and the Chiriqui peaks of Panama.

D.) Plumage.

The few specimens examined have been breeding birds taken in May and June and a good deal worn. Below, the resemblance to *alticola* is very great, although the tone is slightly yellowish and there is practically no white in the ventral region. Above, the back is greenish or pale olive-brown, with heavy, dull black streaks. The head is neutral gray obscured with a brown, similar to the back, and indistinctly streaked with a deeper dusky brown. The lores are obscurely black. The breast and throat are a pale neutral or smoky gray paling in the anal region, and no line of demarkation shows. The bill is flesh-color. The iris is yellow.

Juvenal plumage. Above, much like the adult but browner, especially on the head. The color is a dark, olive-tinged cinnamon, rather broadly streaked with dull black. Below, a yellowish, smoky gray or olive-buff, narrowly streaked on breast, sides, and flanks with dull black. The lores are obscurely dusky; the wing-coverts and secondaries are cinnamon-edged; and the tail is slightly tipped with pale buff.

E.) Discussion.

Junco vulcani is certainly an aberrant species of Junco, for in color pattern it is unlike any of the others. It was described as *Zonotrichia vulcani* (Boucard, 1878, Proc. Zool. Soc. London, p. 57, Pl. iv), and it has a superficial resemblance to this genus, as well as to other tropical genera from which its characters may have been derived. It is probably a survival and is now isolated in a few restricted areas at least 600 miles from the nearest Junco in Guatemala.

SUMMARY

After all, I have little more than touched upon the surface of problems that go much deeper than appearances indicate. The immediate problem before us has been the classification of the Juncos so that names might be applied to the various groups. Instead of accepting the presence or absence of intergradation as a guide by which to separate species from subspecies, I have endeavored to show that species may be recognized by qualitative, and subspecies by quantitative characters. Specific and subspecific characters in most of the Juncos are almost wholly confined to color and therefore by mapping the geographical distribution of color we are able to gain from a new angle a fairly distinct impression of relationships in this genus.

The principle of recognizing qualitative and quantitative characters as specific and subspecific respectively has far-reaching possibilities. Its application is beset with difficulties, for opinions will differ as to the relative

value of characters, but the personal equation must always be reckoned with and it is no greater an obstacle here than elsewhere. There is no conflict with the usually accepted principles of avian evolution, for there are several possible ways of explaining the facts as we find them. The trouble is to name the birds, and I am only pointing out a new and convenient way that adapts itself to conditions actually confronting us and avoids the uniting of dissimilar birds under a specific name because intermediate specimens occur. Even if I am over-estimating the rôle played by hybrids we very much need a nomenclature that will indicate better than at present the intermediate as well as the extreme portions of lines of variation. Zoologists and botanists, by actual experiment, have of late years so revolutionized ideas regarding species and hybrids that systematic ornithologists are likely to be looked upon as backward and unscientific unless they learn more of fluctuations and mutations, of manifestations of Mendelian and other laws, and all the modern theory that goes with them. It is asserted that the criterion for a species is the behavior of the gamete in which unit characters reside. If the union of two gametes carrying the same character gives purity of breed and if two carrying dissimilar characters give hybrids, then the ornithologist of the future has a new and broad field of experiment lying before him. The accumulated facts and theories of the present day will be cleverly fitted together in a new era of synthetical ornithology and converted by experiment into a substantial and enduring edifice well worthy of the labor expended.

Table of Measurements of Juncos (breeding males)

	Specimens	Wing mm.	Tail mm.	Tarsus mm.	Toe (with claw) mm.	Culmen mm.	Depth of bill
							mm.
<i>hyemalis</i>	51	75-83(78.2)	64-71(67.7)	17-22 (20.9)	17-20.5(18.8)	10-12 (10.9)	5.5-6.5(5.9)
<i>carolinensis</i>	27	76-82(79.5)	66-73(70.7)	21-22 (21.5)	17-21 (19.3)	11-12 (11.9)	6-7 (6.2)
<i>aikeni</i>	21	82-91(86.5)	71-83(78.0)	20-22 (21.)	19-21 (19.6)	10.5-13(11.8)	6.5-8 (6.9)
<i>oregonus</i>	18	72-78(74.4)	61-68(64.9)	19-21.5(20.6)	18-20 (18.9)	10-12 (10.9)	5.5-6 (5.9)
<i>thurberi</i>	30	73-80(76.5)	63-70(67.6)	18-21 (19.5)	17-19 (17.8)	9.5-11(10.5)	5-6 (5.6)
<i>couesi</i>	30	73-81(76.9)	63-74(67.6)	18-21.5(20.2)	17-19.5(17.9)	10-11.5(10.7)	5.5-6 (5.8)
<i>pinosus</i>	18	70-74(72.4)	60-69(64.7)	19-21 (19.8)	17-19 (18.1)	10-12 (11.1)	5-6 (5.8)
<i>mearnsi</i>	11	75-81(78.3)	68-72(70.0)	19.5-21(20.5)	18-20 (18.9)	10-12 (11.1)	5.5-6 (5.8)
<i>insularis</i>	28	65-73(69.5)	58-64(61.6)	19-22 (20.1)	17.5-20(18.7)	11.13 (12.2)	6-7 (6.4)
<i>townsendi</i>	28	74-82(78.8)	67-74(70.3)	20-22 (20.9)	17-19.5(17.9)	10-12 (11.1)	5.5-6.5(6.0)
<i>caniceps</i>	14	78-84(81.2)	68-76(72.6)	19.5-21(20.3)	17-20 (18.8)	10.5-12(11.3)	5.5-6 (5.9)
<i>phaeonotus</i>	11	72-83(76.6)	71-78(72.4)	21-24 (22.)	18-20 (18.7)	10-12 (11.3)	6-7 (6.5)
<i>palliatu</i> s	21	74-83(78.2)	69-80(73.4)	20-22.5(21.3)	18-20.5(19.1)	11-12 (11.5)	6-7.5(6.6)
<i>alticola</i>	6	75-78(76.2)	70-77(73.3)	24.5-25(24.7)	21.5-24(22.4)	11.5-13(12.6)	6.5-8 (7.7)
<i>fulvescens</i>	8	69-75(71.2)	62-68(64.5)	20-23 (22.6)	19-21 (20.1)	12-13 (12.8)	7.5-8 (7.9)
<i>bairdi</i>	25	68-74(71.3)	62-69(65.7)	20-22 (21.)	18-20 (18.8)	8-9 (8.7)	6-7 (6.4)
<i>vulcani</i>	12	73-80(76.2)	67-77(71.8)	26-29 (27.6)	21.5-24(22.7)	12.5-14(13.5)	6.5-7 (6.9)

Table of Differential Color Characters of Juncos

	Head	Breast	Back	Sides	Wing-coverts	Tail-feathers	Lores	Iris	Bill
<i>Junco hyemalis</i>	slate	slate	slate	slate	slate	2½ white	slate	brown	flesh
“ “ <i>carolinensis</i>	slate	slate	slate	slate	slate	2½ white	slate	brown	flesh
“ <i>aikeni</i>	slate	slate	slate	slate	white	4 white	slate	brown	flesh
“ <i>oregonus</i>	black	black	brown	pink	slate	2½ white	black	brown	flesh
“ “ <i>thurberi</i>	black	black	brown	pink	slate	2½ white	black	brown	flesh
“ “ <i>couesi</i>	black	black	brown	pink	slate	2½ white	black	brown	flesh
“ “ <i>pinosus</i>	black	black	brown	pink	slate	2½ white	black	brown	flesh
“ <i>mearnsi</i>	ash	ash	brown	pink	ash	3 white	black	brown	flesh
“ “ <i>insularis</i>	ash	ash	brown	pink	ash	3 white	black	brown	flesh
“ “ <i>townsendi</i>	ash	ash	brown	pink	ash	3 white	black	brown	flesh
“ <i>caniceps</i>	ash	ash	red	ash	ash	2½ white	black	brown	flesh
“ <i>phaenotus</i>	ash	smoky	red	brown	red	1½ white	black	yellow	black and yellow
“ “ <i>palliatu</i> s	ash	smoky	red	brown	red	1½ white	black	yellow	black and yellow
“ <i>alticola</i>	ash	smoky	red	brown	red	1½ white	black	yellow	black and yellow
“ “ <i>fulvescens</i>	ash	smoky	red	brown	red	1½ white	black	yellow	black and yellow
“ <i>bairdi</i>	ash	smoky	red	cinnamon	red	2½ white	black	yellow	brown and yellow
“ <i>vulcani</i>	ash	smoky	streaked	brown	brown	0 white	black	yellow	flesh

EXPLANATION OF PLATES

PLATE XI

Species of *Junco*, ventral and dorsal aspects.

- Figures 1 and 1a.—*Junco hyemalis*.
“ 2 “ 2a.—*Junco oregonus*.
“ 3 “ 3a.—*Junco mearnsi*.
“ 4 “ 4a.—*Junco caniceps*.

PLATE XII

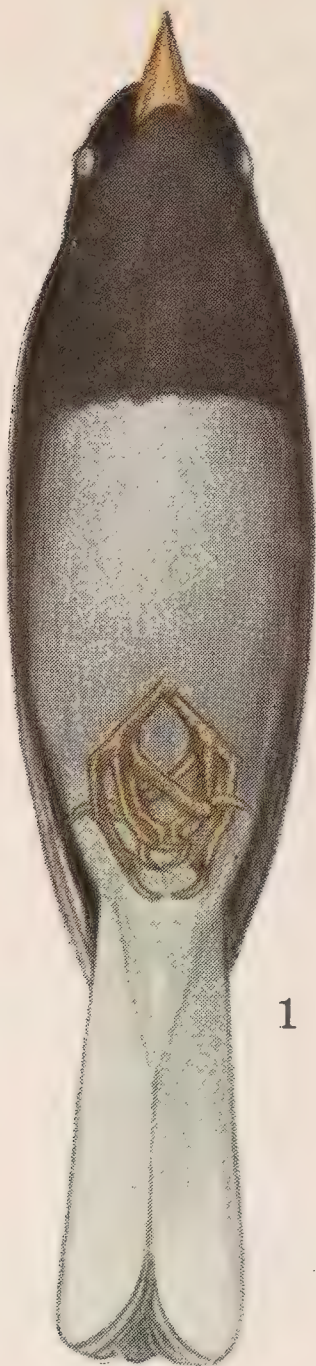
Species of *Junco*, ventral and dorsal aspects

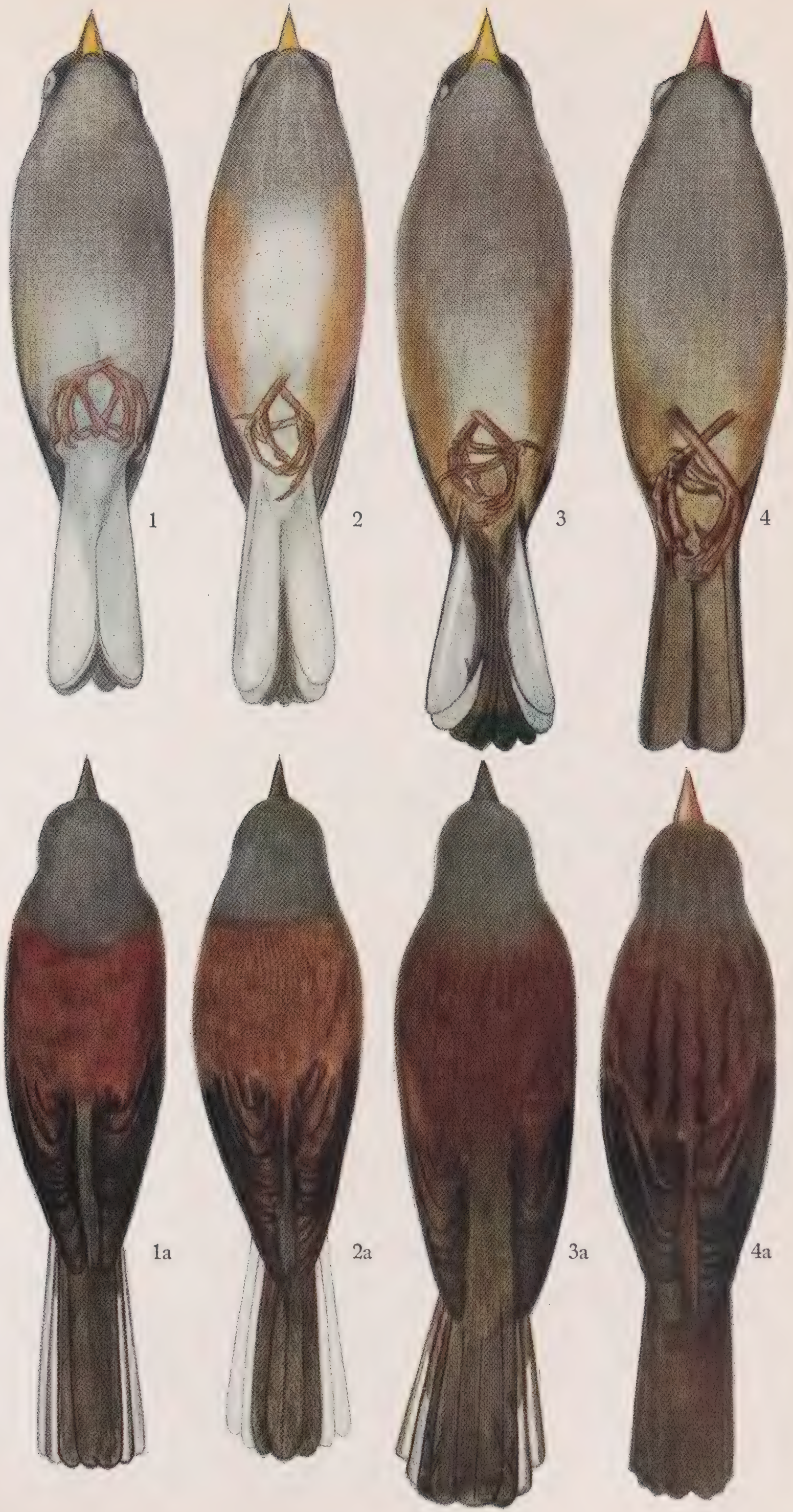
- Figures 1 and 1a.—*Junco phæonotus*.
“ 2 “ 2a.—*Junco bairdi*.
“ 3 “ 3a.—*Junco alticola*.
“ 4 “ 4a.—*Junco vulcani*.

PLATE XIII

Color variation in *Junco oregonus*.

- Figure 1.—*Junco oregonus couesi*, dark average specimen.
“ 2.— “ “ “ light “ “
“ 3.— “ “ *thurberi*, dark “ “
“ 4.— “ “ “ light “ “
“ 5.— “ “ *oregonus*, dark “ “
“ 6.— “ “ “ light “ “





SPECIES OF JUNCO



1



2



3



4



5



6

JUNCO OREGONUS



**Article X.—THE AMPHIBIANS COLLECTED BY THE
AMERICAN MUSEUM EXPEDITION TO
NICARAGUA IN 1916**

BY G. K. NOBLE

PLATES XIV TO XIX

INTRODUCTION

The collections of reptiles and amphibians in the American Museum from southwestern United States and the West Indies have been rapidly growing during the past five years. As the work on these collections progressed, the need for material from related faunal areas was keenly felt. Small collections from Mexico and Costa Rica had been received through purchase or gift, but there was no extensive collection with which to trace out the many problems of zoogeographical relationships which arose in connection with the other work. In May 1916, through the kindness of Dr. Bashford Dean, a generous grant from the Cleveland H. Dodge Fund was made available to the Department. Nicaragua was selected as the region which would yield the best results for intensive study. Nicaragua had not been visited by a herpetologist for a long time. It was perhaps the least known of the large republics of Central America. The types of most of the species described from Nicaragua were in the United States, and would be available for comparison with fresh material. It was felt that a study of the herpetological fauna of Nicaragua would be the most satisfactory not only to the American Museum, but to other museums as well.

The work of the expedition was primarily herpetological and ichthyological. Mr. Clarence R. Halter, assistant in herpetology at the American Museum, and Mr. L. Alfred Mannhardt, assistant in zoology at Yale University, were given charge of the expedition. These men made extensive field notes, and took many photographs, some of which are published here. After the expedition had been in the field several months, the Department decided to extend its activities to a more complete survey of the Republic. The additional expenses involved were met by a special appropriation. The success of the expedition was due largely to the untiring efforts of the collectors during their stay in Nicaragua.

The present paper deals with the amphibians collected by the expedition. It is only a preliminary report. The larger problems of zoogeographical distribution have been left for a later paper, in which the distribution of the

reptiles also will be discussed. This paper is, however, complete, in that it considers all of the species of amphibians collected.

While few generalizations have been made, the remarks on the distribution of some of the species are intended to suggest the larger problems of zoogeography. Several species are reported from Nicaragua for the first time. At least one of these species, *Leptodactylus albilabris*, may have been introduced. Two species are described as new. Many of the species are rare in collections. *Hyla boulengeri* was formerly known only from the type specimen. Some mention has been made of the breeding periods of the batrachians. The breeding period of several of these has been determined by an examination of the genital organs of a large series of specimens. This work would have been useless if the collectors had not given exact dates. In herpetology it is just as important as in ornithology to record the date of collecting, but many collectors in the past have failed to realize this.

No attempt has been made to give complete synonymies. For each species a reference to the original description and another to the *Biologia Centrali-Americana* are given. Günther has been accepted as the most recent reviser, and it is only when material changes are made in his work that additional references are mentioned. References to the literature which Günther has apparently overlooked are included in the synonymies. References are also given to all very recent literature bearing on the Central American amphibians discussed.

I take pleasure in acknowledging the kind assistance of Dr. Leonhard Stejneger who gave me every facility for studying the Central American amphibians at the National Museum. To Mr. H. W. Fowler I am indebted for the opportunity of examining the Central American amphibians at the Philadelphia Academy of Natural Sciences. I am also obliged to Dr. A. G. Ruthven of the University of Michigan for the loan of a series of *Leptodactylus albilabris*. Dr. William M. Wheeler, Dean of the Bussey Institution, has kindly identified the ants which made up a large part of the stomach contents of the various amphibians collected. Dr. J. Bequaert of the American Museum has examined other insects at my request.

Itinerary

A complete account of the region traversed by the expedition will be given in a later paper. In order to make clear the localities in which amphibians were taken, an itinerary has been extracted from the field notes of the collectors. In this brief outline of the trip references to life zones have not been given, and mention of habitats and amphibian associations have been left for another part of the paper.

On May 31, 1916, the expedition left New York for Bluefields, Nicaragua, via New Orleans. The members reached Bluefields June 17, and four days later left the town for the nearby Maselina Creek, where they hoped to secure better collecting facilities than were available in the immediate environs of Bluefields. By July 1 preparations were complete for a collecting trip into the interior. Both Mr. Halter and Mr. Mannhardt went north as far as the Rio Grande and continued up that river one hundred and twenty-five miles until they reached Sioux Plantation on Sixicuas Creek. They spent from July 4 to 10 at this locality and then dropped down the river to Cooley Plantation. They returned to Bluefields July 28 and made arrangements for a trip to the region just north of that town. On August 1, the expedition started for Cukra. Several days were spent in collecting at Kanawa and Wholesome Creek, but most of the time was spent at Cukra proper. On August 22, the party returned to Bluefields, and on August 27 started south again to Maselina Creek. The expedition remained in this vicinity until September 27, although different members made a number of short trips back to Bluefields.

Arrangements were at last complete for a more extended investigation. On September 27 the expedition divided, Mr. Halter going at once south to the San Juan River, and Mr. Mannhardt, after a week's delay, starting north for the Prinzapolka River. Mr. Halter reached Barra del Colorado on September 28 and made large collections in the vicinity until October 17, when he was able to engage a boat to take him west across Nicaragua. In the meantime, Mr. Mannhardt was progressing slowly up the Prinzapolka toward Eden Mine. He collected on many of the affluents of that river, but chiefly on the Cupitna and Pia Creeks. Consequently, he did not reach the headwaters of the river system until November 10. It is there that Eden Mine is located. Mr. Mannhardt made it his base and began an intensive study of the fauna in this mountainous part of Nicaragua.

By November 10 Mr. Halter had reached Tuli Creek, which flows into the southeastern part of Lake Nicaragua. He had reached San Carlos October 30, the mouth of Tuli Creek on November 3, and by November 10 had started up the creek toward the Chontales Mountains. Mr. Halter did not return to the mouth of the creek until December 4. He then proceeded to San Miguelito and collected in the vicinity until January 4. Then followed a hasty trip to Managua and the western bank of the lake. The return trip across the lake and down the river San Juan allowed few opportunities for study, and no amphibians were collected. Mr. Halter reached Bluefields January 31, to find that Mr. Mannhardt had completed his survey of northern Nicaragua and had returned to the States on December 11. Mr. Halter left for New York on February 3, 1917.

Topography and Vegetation

Most of the localities visited presented a complex of habitats and amphibian associations. The most striking features of the habitats are given below under their respective localities, but a consideration of special habitats has been left for the annotated list of species.

MASELINA CREEK meanders through a flat coastal plain which is nearly at sea-level. The region is a vast mangrove swamp with here and there islands of dry land in which palms and huge trees take root. The creek partly overflowed its banks during the collector's stay, for it rained nearly all of the time.

SIoux PLANTATION, on the Rio Grande, presented a very different appearance. Its altitude is only about seventy-five feet, but savannahs instead of lowland forests prevail. Some patches of bamboo occur along the river, and a few flamboyants and other conspicuous trees are present. The soil contains much clay. Outcroppings of rock are rare. The temperature averaged about 85° during part of July. There was little rain, and all the vegetation showed signs of drought. The thatching of the native huts retained a little moisture and afforded a retreat for some of the amphibians, chiefly for *Hyla baudinii*.

COOLEY PLANTATION, on the same river, is about twenty-five feet lower in altitude than Sioux Plantation. The vegetation was much the same in the two regions, but at Cooley Plantation scrub growth prevailed instead of savannahs.

CUKRA is a village near Kanawa and Wholesome Creek. The elevation of the region is about one hundred feet. No swamps occur, although there are several streams. The savannah grasslands are broken by clumps of forests and thickets. Many of the latter are probably of second growth. It rained considerably during the collector's stay in the region, and a number of shallow savannah ponds were formed.

CUPITNA CAMP is a lumber base on one of the affluents of the Prinzapolka. The camp is situated in the heart of a mahogany forest. The dense jungle of this region is similar to that of most of the upper Prinzapolka. Some patches of grass occur along the river banks, but there are no savannahs.

EDEN MINE is situated in the hilly country of northern Nicaragua. The region varies in altitude from six hundred to over a thousand feet above sea-level. The valleys about Eden Mine are filled for the most part with shady, open woods. There are some wet forests, but very few swamps occur. A large part of the woods in the vicinity of the mine has been destroyed to form artificial clearings, which support a poor amphibian fauna.

COLORADO BAR is in northeastern Costa Rica at sea-level. A dense

jungle of large trees extends almost to the water's edge. Many swamps wind tortuously through the jungle. The faunal and floral life is typical of a tropical forest.

SAN CARLOS, on Lake Nicaragua, is surrounded by extensive swamps. Its altitude is about one hundred and ten feet, but there are many knolls and small hills which rise to a greater height above sea-level. Lowland forests and forest ponds support a fauna which is not unlike that of the adjacent region to the north.

SAN MIGUELITO, on Lake Nicaragua, was used as a base for exploration in the west. The altitude is about one hundred and ten feet. Many hills arise behind the town. These finally unite to form the low range known as the Chontales Mountains. The sides of the hills near San Miguelito are bare. A desert vegetation made up chiefly of cacti abounds. Some bamboo occurs on the river banks, but no forest trees are found. The Chontales Mountains are covered with dense forests similar to those of Tuli Creek.

TULI CREEK, to the south of San Miguelito, supported a large amphibian fauna. The stream has its headwaters in a series of swamps. Dense tropical forests extend for about fifteen miles on either side of the creek. It rained considerably during the collector's stay in the region, and the swamps encroached widely upon the forests.

ANNOTATED LIST OF SPECIES

1. *Rana austricola* (Cope)

Plate XV, Fig. 1

- Rana halecina austricola* COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 517.
Rana virescens austricola WERNER, 1896, Verh. Ges. Wien, XLVI, p. 349. IVES, 1891, Proc. Acad. Nat. Sci. Phila., p. 461.
Rana lecontei MOCQUARD, 1899, Bull. Soc. Philom., (9) I, p. 158.
Rana halecina BOETTGER, 1892, Kat. Senck. Ges. Batr., p. 6. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 198. WERNER, 1903, Abh. Bayer. Ak., XXII, 2, p. 341. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194.
Rana austricola RUTHVEN, 1912, Zool. Jahrb. (Syst.), XXXII, p. 305.

Fourteen specimens from several widely separated localities, most of them from Tuli Creek, Eden Mine, and Maselina Creek.

These specimens agree very well with a series of *R. austricola* in the Philadelphia Academy from Hidalgo, Mexico (A. N. S. P., 14615-14616) and another from Mexico City (A. N. S. P., 14605-14614). Several of the Hidalgo specimens are very dark and are similar to two of our specimens from

Greytown on the San Juan River. These two specimens are darker than any of our others and their snouts are less acuminate, but not so blunt as the snout of *R. palmipes*. This bluntness of snout does not seem to be due to any artificial cause. Barbour (1917, Proc. Biol. Soc. Wash., XXX, p. 103) has shown that the snout of *Leptodactylus albilabris* may be more or less depressed. Apparently the snout of *R. austricola* may be more or less pointed within a certain range. The two specimens in our series with most acuminate snouts are adults of opposite sex. Their gonads are not very large. The two specimens with the bluntest snouts are females with ovaries distended with ova. The difference in head form does not seem to be correlated with sex. It may be dependent upon season or habitat, but without a very large series this would be difficult to determine.

The variation in color is not limited to an intensifying or fading of the tones. There is also a slight variation in pattern. The spots on the back may be more or less confluent. In the smallest and the largest specimens in the collection the spots have been extended to form an unbroken but irregular streak on each side of the back. Each pair of spots may be confluent in a transverse direction, but it is more common for the spots in each longitudinal row to run together. There does not seem to be any progressive development of pattern during the growth of an individual, for specimens of the same size may have very different color patterns.

Two females were taken with their bodies swollen with ova, one on November 18 at Eden Mine and the other on August 17 at Cukra. It is possible that the breeding season of the species extends over several months, but it is more probable that the breeding season varies slightly with each locality. The females are larger than the males. An average pair differ in the proportion of 84:70. Only a few of the stomachs examined contained food. This consisted chiefly of spiders and weevils.

2. *Rana palmipes* Spix

Plate XIV

Rana palmipes SPIX, 1824, Nov. Spec. Test. Ran., p. 29, Pl. v, fig. 1. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 202. RUTHVEN, 1912, Zool. Jahrb. (Syst.) XXXII, p. 306. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194.
Rana chrysoprasina Deckert, 1915, Zoologica, II, No. 1, p. 20 (*nec* Cope, 1866).

Thirty-five specimens from several localities in the eastern drainage systems: Eden Mine, Cupitna and Pia Creeks, Cooley Plantation on the Rio Grande, and Cukra.

The specimens in this series correspond exactly with those of a series from Guatemala and those of another series from Mexico in the National Museum. The variation in color of our specimens is limited to the fading out of the ground tone and to the developing of spots on the posterior part of the back. In life the color above was grass-green from the tip of the snout to the tympanum and olive from the tympanum to the ends of the appendages. In certain lights a bronze-like shimmer was present on the head. The posterior sides of the legs were mottled with dark brown and white. The lower parts of the legs were less distinctly mottled with brown. The throat was pearly white; the belly and ventral surfaces of the appendages were washed with lemon yellow. The posterior appendages were heavily mottled with brown below.

There is considerable variation in the size of the tympanum in *R. palmipes*. This is apparently not correlated with sex or habitat. Two adult females of identical size, measuring 95 mm. from snout to vent, were captured together in a swamp near Eden Mine. These specimens have the ova equally well developed. The difference in size of the tympanum is very distinct.

	A.	B.
Greatest length	10.0 mm.	8.5 mm.
Greatest width	8.5	7.5

R. palmipes was always found in the vicinity of water, generally in long grass by the edge of some marsh or pond. Five females with ovaries greatly distended with ova were taken near Eden Mine on November 22. Another specimen in the same condition was taken November 23. A young one with the tail not yet absorbed was taken the same day. These data suggest that the breeding period of the species in the vicinity of Eden Mine occurs about the end of November, and that the larva takes about one year to complete its metamorphosis. Females from other localities at an earlier date did not have the ovaries enlarged.

The sexually mature female is much larger than the male. The body length of an average female is 89 mm. from snout to vent, while that of the male is only 72 mm.

R. palmipes apparently takes a variety of food. The stomachs examined contained, for the most part, spiders and insect larvæ. One large specimen of *R. palmipes* had eaten a young one of the same species. A large amount of extraneous wood and grass was contained in the stomach with the young frog. Another specimen which was caught in a swamp near Eden Mine disgorged a small fish when killed with an alcohol injection.

The smallest specimen of *R. palmipes* in the series measures 27 mm. from

snout to vent, and possesses a rudiment of a tail 6.5 mm. in length. It was interesting to find in this specimen that the two halves of the epicoracoid cartilages were firmly attached and did not allow any free movement. The girdle had become firmisternal before the sternum and xiphisternum were distinguishable from the tissue connecting the abdominal muscles and before the omosternum showed evidence of any bony deposit.

3. *Rana cæruleopunctata* Steindachner

Rana cæruleopunctata STEINDACHNER, 1864, Verh. Ges. Wien, p. 264, Pl. xv, fig. 1.

BOULENGER, 1882, Cat. Batr. Sal. Brit. Mus., p. 50. GÜNTHER, 1900, Biol.

Centr.-Amer., Batr., p. 205. FOWLER, 1916, Proc. Acad. Nat. Sci. Phila., p. 396.

Ranula cæruleopunctata COPE, 1866, Proc. Acad. Nat. Sci. Phila., p. 130.

Trytheropsis chrysoprasinus COPE, 1868, Proc. Acad. Nat. Sci. Phila., p. 117; 1876, Journ. Acad. Nat. Sci. Phila., VIII, p. 114, Pl. xxiii, fig. 12.

Ranula chrysoprasinus COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 276 (*nec* Cope 1866); 1887, Bull. U. S. Nat. Mus., XXXII, p. 19.

Twenty-two specimens from several widely scattered localities along the east and west drainage systems: Eden Mine, Pia, Cupitna, Sixicuas, Mase-lina, and Tuli Creeks.

Günther, with little evidence, placed *Rana chrysoprasina* in the synonym of this species. Sufficient evidence is not available to show conclusively that *chrysoprasina* is distinct, but at least it is very probable that *chrysoprasina* does not occur in Nicaragua. I have examined in the National Museum the four young specimens sent from Nicaragua by Dr. Bransford and referred by Cope (1887, p. 19) to *chrysoprasina*. These specimens are in poor condition. They are indistinguishable from *cæruleopunctata*. The specimen which Cope (1876, Pl. xxiii, fig. 12) figured as *chrysoprasina* is also poorly preserved. The large yellow spots on the thighs represent all that is left of the color pattern. The short webbing of the toes and the long snout are typical of *cæruleopunctata*. Another specimen recorded as *chrysoprasina* was sent from San José, Costa Rica, by Van Patten. It is now in the Philadelphia Academy (No. 2153). This specimen is apparently identical with *cæruleopunctata*. The three specimens from Costa Rica recently referred by Deckert (1915, Zoologica, II, No. 1, p. 21) to *chrysoprasina* have been deposited in the American Museum (Nos. 3815-3817). They are identical with our specimen of *R. palmipes* from Nicaragua and should have been referred to that species. In spite of these faulty records, it is still possible that *chrysoprasina* is a valid species.

The type of *chrysoprasina* was sent to the National Museum from Arriba, Costa Rica, by Charles N. Riotte. Cope described the species, but whether

he ever returned the specimen to that museum is not known. At present, the type cannot be found in that institution. Cope actually compared his type with some specimens of *cæruleopunctata*, for he says in the original description (1866, p. 130) of *chrysoprasina*:

This species is allied to the last, but has a relatively shorter muzzle and limbs. Nostril nearer end of muzzle than orbit (equidistant in *cæruleopunctata*), heel to middle of loreal region. Toes fully, not widely palmate, three distal phalanges of fourth free. . . .

Steindachner represents much less palmation than exists in our specimen.

Cope described the color of *chrysoprasina* as "brilliant leek-green, the groin and belly approaching golden." The coloration of *cæruleopunctata* is entirely different. It is possible that Cope had an aberrant specimen of *R. palmipes*. Without further information it is most conservative to allow *chrysoprasina* to stand as valid.

Some of the color in our specimens has apparently faded in alcohol. The color pattern and ground tones are the same as those described for the species. In life, the dark spots on the back were greenish. The concealed portions of the legs, below the spotted pattern, were brilliant red; the ventral surfaces of both anterior and posterior appendages were pinkish. The ends of the toes were red, like the concealed parts of the legs. Most of these reds have changed to white in alcohol.

The ground tones have not changed in alcohol, but these vary somewhat in the different specimens in our series. This variation is confined on most of the body to a general intensifying or fading of color. The yellow spots on the posterior sides of the thighs undergo variation with age. While this variation is not always consistent, it does follow a rather definite plan. In the smallest specimens there are no light spots on the thighs, but the posterior surfaces are pink and are crossed by three dark bars. This blackish pigment gradually encroaches upon the light areas as the individual matures. The pinkish areas change to yellow. Medium-sized specimens have two light spots between the three bars, and a third spot distal to the outer bar. In older specimens the black has increased and has cut the spots in two. The spots seem to divide by fission, like so many amoebæ. Three pairs of spots occur in several of the larger specimens. Sometimes an additional pair of spots is present. The development of color pattern does not progress evenly in all cases. The multiplication of spots may not take place. For example, two adults females in the series are of identical size, measuring 59 mm. from snout to vent. They both have ovaries distended with large ova, and both were taken in the same locality. Yet one specimen has only two yellow spots on one thigh and three on the other, while the other specimen has eight spots on each thigh. There is an apparent sexual difference.

The males, which are much smaller than the females, have the smaller number of spots.

Rana cæruleopunctata was very rare along the low flat coastal regions such as those through which Maselina Creek flows; but it was often seen in the mountainous regions of northern Nicaragua and in the hilly country near Tuli Creek. *R. cæruleopunctata* is a frog of the dense jungle. It was found chiefly on the ground among dead leaves in damp, shady places. One pair was taken November 23 while in embrace. Other specimens, taken between this date and December 1, had the ovaries greatly distended with ova. The breeding season of the species in the vicinity of Tuli Creek must therefore be about the end of November. There is a decided difference in size between the sexes. The female of the pair taken in embrace measures 58 mm. from snout to vent, while the male measures only 40 mm.

4. *Dendrobates tinctorius* (Schneider)

Calamita tinctorius SCHNEIDER, 1801, Hist. Amphib., p. 175.

Dendrobates tinctorius BOULENGER, 1882, Cat. Batr. Sal. Brit. Mus., p. 142. COPE, 1887, Bull. U. S. Nat. Mus., XXXII, p. 19. PERACCA, 1896, Bol. Mus. Torino, XI, No. 253, p. 11. DECKERT, 1915, Zoologica, II, No. 1, p. 22. FOWLER, 1916, Proc. Acad. Nat. Sci. Phila., p. 396.

Dendrobates tinctorius auratus COPE, 1893, Proc. Amer. Phil. Soc., XXXI, p. 340.

Hylaplesia tinctoria GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 207.

Dendrobates amænus WERNER, 1901, Verh. Ges. Wien, LI, p. 627.

Two adult specimens from Tuli Creek.

Werner (1901, p. 631) has recently revised the Dendrobatidæ, and has described a new species of *Dendrobates* from Costa Rica. In his key he distinguishes this species, *amænus*, from *tinctorius* by a difference in leg length, the tarso-metatarsal articulation in the former species reaching beyond the end of the snout. The legs of our specimens are proportionately as long as those of *amænus*, but it does not seem to me that leg length in this case is a specific character. Werner, in his description of *amænus*, says: (translation) "the tarso-metatarsal articulation reaches the nostril, the end of the snout, or beyond." This would cover the range of variation exhibited in other specimens of *tinctorius* in this museum. Three of these specimens are from British Guiana, one from Colombia, and one from Costa Rica. Our two Nicaraguan specimens have the tarso-metatarsal articulation reaching only slightly beyond the snout. I have examined two specimens of *tinctorius* from Taboga Island. These were collected by James Zetek and are now in the National Museum (Nos. 51955-51956). They are indistinguishable from our two Nicaraguan specimens. The Taboga

Island specimens are topotypes of *D. auratus*. If the Central American race is distinct from the South American, it will have to receive a new name, for Boulenger (1913, Proc. Zool. Soc. London, p. 1026) has shown that the type probably came from Guiana. The first available name for the Central American form would be *auratus*, but we have not enough evidence to separate the Central American form. Our Costa Rican specimen is identical with the Nicaraguan specimens and Werner's description of *amænus* agrees well with either these specimens or our Guianan specimens. The color varies somewhat in all of the specimens, but very little is known about color variation in the green and black variety of *tinctorius*.

Boulenger, in discussing the color varieties of *tinctorius*, has said (1913, *op. cit.*, p. 1028):

The numerous varieties of *Dendrobates tinctorius* are much in want of revision. Among those already described there is one which is unquestionably entitled to specific rank, and for which I wish to propose the name *D. paraensis*. Disks of fingers and toes much larger than in *D. tinctorius*; a small but very distinct tubercle on the inner side of the tarsus, nearer the metatarsal tubercles than the tibio-tarsal articulation.

One specimen of *tinctorius* in the American Museum (No. 3139) from Jimenez, Colombia, was purchased from Rosenberg. Since it was identified by Boulenger as *tinctorius*, it probably represents what he considers the typical form. Moreover, its digital expansions agree very well with Boulenger's (1913, *op. cit.*, text fig. 178) figure of those of *tinctorius*. The three specimens in the American Museum from Guiana were collected near Georgetown by Rodway. The digital expansions of these specimens are much larger than those of *D. paraensis* as figured by Boulenger (1913, *op. cit.*, text fig. 178). The digits of both Guianan and Colombian specimens differ from the Central American specimens in having the dorsal surface covered by two distinct disks. In the Nicaraguan specimens there is some evidence of disks, but their posterior edges are fused with the rest of the integument. There is considerable difference in the exact form of these digital disks. In the Guianan and Nicaraguan specimens they are elongate, while in the Colombian specimen they are round, as figured by Boulenger. With the small series of specimens of *tinctorius* available for study, it is impossible to determine the systematic status of the species in Central America. Further work may show that the form of the digits represents a good character by which to distinguish the Central American race.

The arrangement of the black spots varies greatly in the Central American specimens. These spots are arranged in life upon an iridescent blue-green ground color. Both of the Nicaraguan specimens were captured during a shower and both about ten o'clock in the morning. They were found among

the leaves on the floor of the forest which surrounds Tuli Creek. One specimen was taken November 7, and the other November 21.

The stomachs of these two specimens contained mostly ants, although a few beetles and other insects were present. There were about fifty ants in each stomach. Dr. Wheeler has identified most of these as *Wasmannia auropunctata* Rog. Seven other genera were represented, but each by only a few workers: *Strumigenys*, 2 sps.; *Rhopalothrix*, n. sp.; *Leptogenys* (*Lobopelta*), sp.; *Trachymyrmex*, sp.; *Ponera*, sp.; *Pheidole*, 2 sps.; and *Solenopsis*, sp.

5. *Dendrobates typographus* Keferstein

Dendrobates typographus KEFERSTEIN, 1867, Gött. Nachr., p. 360. DECKERT, 1915, Zoologica, II, No. 1, p. 22. WERNER, 1901, Verh. Ges. Wien, LI, p. 630.
Hylaplesia typographa GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 207.

Taken only in the southeastern part of Nicaragua and the northeastern part of Costa Rica: thirty-two specimens from the region about Cukra, two from La Hunter, and three from Colorado Bar.

Werner (1901, p. 630), in his revision of the Dendrobatidæ, describes the tympanum of this species as (translation) "very small, much smaller than the disks of the fingers." In our series, the tympanum is always larger than the disks of the fingers, but sometimes the dorsal half of the tympanum may be undifferentiated from the temporal region, making the tympanum appear like a small crescent.

In alcohol, the color of all but two or three of our specimens is a metallic blue. The dorsal and lateral surfaces of the specimens are washed with a pearly gray and spotted with dark blue. In a few of the specimens the pearly gray is replaced by a pink. The color, in all but these pink specimens, has been greatly modified in alcohol.

In life, the color of the head and body was a brilliant carmine. A few dark blue spots were generally present on the back. In practically all of the specimens from Cukra and Colorado Bar the appendages were a brilliant blue. The two specimens from La Hunter had only the lower half of the appendages, from the humerus and femur down, washed with blue. A blue patch was generally present on the sacral region. The two specimens from La Hunter had the entire dorsal surface excepting the appendages tinged with brilliant carmine, but the dark blue spots appeared soon after the specimens had been killed in formalin. The ventral surface of the specimens was variable, blue, carmine, or a pearly gray predominating in different individuals. Four young specimens from Cukra, averaging 12.5 mm. from snout to vent, were very different in coloration from the adults,

which were 22 mm. long. The dorsal surface was very dark red, clouded with dark brown. The ventral surface was a dark blue. Dark blue spots appeared on the dorsal surface after death.

All of the specimens were caught in damp, shady situations near the water. They were found under leaves and pieces of decaying wood which were strewn about on the ground. Only a few stomachs were examined. They contained mostly small red ants. One pill bug and a spider were found with the ants.

6. *Leptodactylus pentadactylus* (Laurenti)

Plate XV, Fig. 2

Rana pentadactyla LAURENTI, 1768, Syn. Rept., p. 32.

Leptodactylus pentadactylus GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 212.

Four specimens, varying in size from 34 to 134 mm. from snout to vent, all taken in the eastern side of the Republic: Eden Mine, Sioux Plantation, and Maselina Creek.

The smallest specimen is from Eden Mine, the most northerly point on the mainland from which the species has been recorded. It has been known from the island of Dominica, B. W. I., for a long time, but never so far north on the mainland. The largest specimen taken at Maselina Creek shows the transverse cross-bars on the back. These are absent in the two medium-sized specimens. In the smallest specimen the interorbital bar and a supratympanic spot are present as well as the labial bars. All of the specimens but the largest one have the ventral surface dark brown spotted with white — the characteristic coloration of the immature. In all of the specimens there was, in life, a considerable amount of red on the thighs. In most alcoholic specimens of *L. pentadactylus* which I have examined the red has faded out, but this bright tone is evidently very striking in life.

Two of the specimens were caught in the morning. One was taken in a hut at Maselina Creek, and the other was found under a pile of boards near the edge of a house at Sioux Plantation. It is evident that *L. pentadactylus* is accustoming itself to human habitations. The stomach of the largest specimen contained several cockroach wings; fragments of the legs, wings, and heads of grasshoppers; one spider; and a large amount of vegetable material.

7. *Leptodactylus albilabris* (Günther)

Cystignathus albilabris GÜNTHER, 1859, Ann. Mag. Nat. Hist., (3) 4, p. 217.

Leptodactylus labialis IVES, 1891, Proc. Acad. Nat. Sci. Phila., XLIII, p. 461.

Leptodactylus albilabris GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 213. STEJNEGER, 1904, Rept. U. S. Nat. Mus., 1902, p. 561, figs. 6-10. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194. RUTHVEN, 1912, Zool. Jahrb. (Syst.), XXXII, p. 307. BARBOUR, 1914, Mem. Mus. Comp. Zool., XLIV, No. 2, p. 255; 1915, Proc. Biol. Soc. Wash., XXVIII, p. 72; 1917, Proc. Biol. Soc. Wash., XXX, p. 103.

Several hundred specimens from many localities in the east and the west; most of the specimens from the headwaters of Tuli Creek.

Besides this huge series, I have examined a number of specimens collected in Mexico by Dr. A. G. Ruthven and have compared these mainland specimens with the large series of specimens in the National Museum from Porto Rico and the neighboring islands. With these large collections it has been possible to determine something of the range of variation in mainland and island specimens, but it has not been possible to shed much light upon the original home and subsequent migration of the species.

There are many differences between the mainland and island specimens. In a series of a hundred specimens from both regions, there are many individuals which are very unlike but others which are so similar that no one distinguishing character can be given. Three characters may be used to distinguish the average mainland specimen from the average island specimen. The dorsal surface of the legs distal to the femora is covered, in the island specimens, with numerous sharp-pointed rugosities, while in the mainland specimens these tubercles are less numerous and blunt — in some cases they may be absent. The brown spots which form the dorsal color pattern in the mainland specimens are rarely or never outlined with white, while in island specimens white is often present and sometimes very distinct. The throat of the mainland specimens is either white or is stippled around the edges with dark brown. In the island specimens the throat may be entirely washed with brown. These differences are not constant; they probably represent nothing but local variations. The Nicaraguan specimens generally have the ventral surface of the thighs slightly spotted, while the Mexican specimens generally lack the spots. Island specimens probably differ from the mainland specimens because of a difference in environment rather than because of ancient isolation.

It is indeed strange that, in spite of all the collecting which has been done in Central America, *L. albilabris* has never before been taken south of Mexico. Bransford, McNeil, Stimpson, and others collected in Nicaragua; and yet they never took this species. It does not seem probable that the species could have been overlooked, for Stejneger (*op. cit.*, p. 562) had said "it is one of the commonest, most obtrusive, and most easily caught batrachians wherever it occurs." Is it possible that the species has been confused

with *L. melanonotus* and *L. caliginosus*? No evidence is available to show that this is the case. We must, then, assume that *albilabris* in recent years has been rapidly extending its range southward. It is probable that *L. pentadactylus* has recently extended its range northward. Both species may have been introduced by man, but here again we can only conjecture. If it is proved that they have been introduced by man, the argument (see Barbour, 1914) in favor of the introduction of *L. albilabris* into Porto Rico by human agency is greatly strengthened. In both Porto Rico and Nicaragua the foreigner has adapted itself entirely to the new country, reminding us in this respect of our own English sparrow.

8. *Leptodactylus melanonotus* (Hallowell)

- Cystignathus melanonotus* HALLOWELL, 1860, Proc. Acad. Nat. Sci. Phila., p. 480.
Leptodactylus melanonotus BROCCHI, 1882, Miss. Sci. Mex., Batr., p. 20. BARBOUR, 1914, Mem. Mus. Comp. Zool., XLIV, No. 2, p. 254.
Leptodactylus caliginosus MOCQUARD, 1899, Bull. Soc. Philom., (9) I, p. 163. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 214. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194. ATKINSON, 1907, Ohio Naturalist, VII, p. 151. RUTHVEN, 1912, Zool. Jahrb. (Syst.), XXXII, p. 306.

More than a hundred specimens from many localities on both the east and the west sides of the Republic; most from the vicinity of Tuli Creek.

I have compared this large series with a specimen of *L. caliginosus* in the American Museum from Merida, Venezuela, and heartily agree with Barbour (*loc. cit.*) that *L. melanonotus* is perfectly distinct from that species. Little has been said of the variation in *L. melanonotus*, for most authors have considered the Central American species synonymous with the wide-ranging *L. caliginosus*. Most of our specimens were taken in swamp-lands. The color pattern is obscured by the very dark ground tones. In several specimens from Eden Mine the ground color has faded to a gray brown and a color pattern has appeared, consisting of a dark interorbital bar edged anteriorly with light gray and a number of dark spots on the back and lips. A few dark spots on the legs tend to form transverse bars. Even in the lightest specimens this color pattern is indistinct. The throat and edges of the belly are reticulated with dark brown in all specimens. This ventral coloration serves as an excellent field mark for distinguishing *L. melanonotus* from *L. albilabris*. In most adult specimens the white interstices of the dark reticulations on the posterior surfaces of the thighs change to an orange, simulating the coloration in *L. pentadactylus*, but in many adult specimens the orange is wanting. This condition is apparently not correlated with sex.

The most striking external character of *L. melanonotus* is the longitudinal rows of warts which sometimes appear in adult specimens. These are of most common occurrence in very large females but females of equal size and having ova equally developed may or may not have warts. Males and females may have exactly the same degree of wartiness, or they may entirely lack the tubercles. Wartiness is not correlated with sex in this species. Two very large females from the same general locality, with ova well developed, are strikingly different, one having eighteen rows of warts and the other none. The wartiness of *L. melanonotus* is probably due to some stimulus in the environment.

9. *Syrrhophus ridens* (Cope)

Phyllobates ridens COPE, 1866, Proc. Acad. Nat. Sci. Phila., XVIII, p. 131.

Syrrhaphus ridens GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 216.

Three adult specimens from the vicinity of Tuli Creek and one from Cupitna Camp.

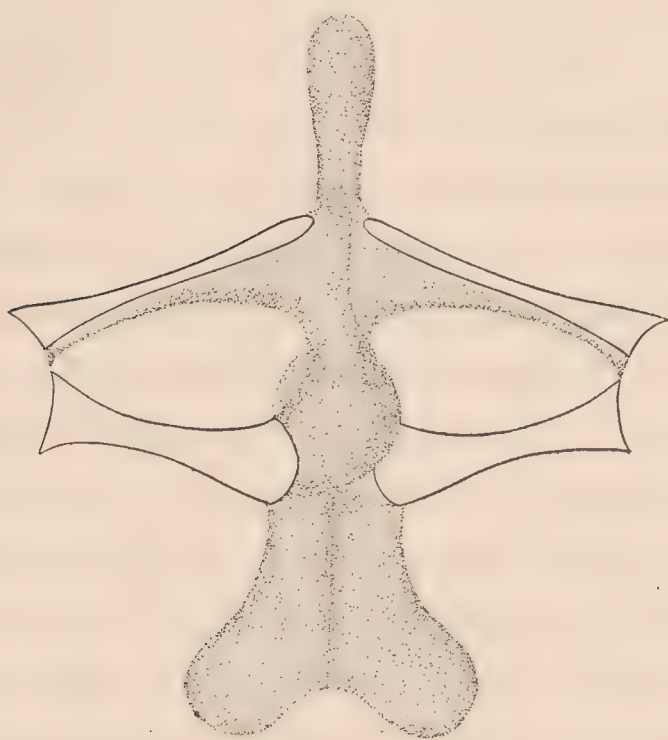


Fig. 1.

Fig. 1. Pectoral girdle of *Syrrhophus ridens* (Cope).

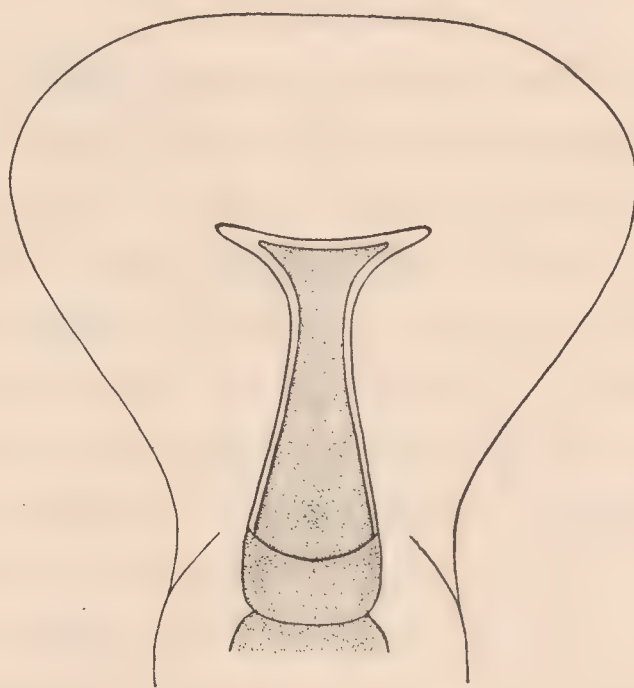


Fig. 2.

Fig. 2. Terminal phalanx of *Syrrhophus ridens* (Cope).

Cope, at the beginning of the original description of the species, says:

The close areolation of the abdomen, throat, and lower face of the femora, the recurved angle of the mouth, the minute ($\frac{1}{8}$ orbit) tympanum, above the ordinary position, the truncate tongue are marked features in this species.

In the two largest specimens before me the ventral surface is entirely smooth; in the smallest it is slightly granular. The tympanum of three of the specimens is about one-fourth the diameter of the eye; the tympanum

of the smallest specimen is about one-sixth. The specimens agree fairly well with the original description in all other particulars. The color pattern is subject to some variation, but in two of the specimens it is nearly the same as that described for the types. In one of these specimens there are only two, not three, dark bars across the femora. Cope does not mention the color of the posterior faces of the thighs. This is dark brown in all of the specimens. The smallest specimen differs from the others in having a white vertebral stripe.

The type locality of *S. ridens* is the San Juan River, Nicaragua. Our specimens are practically topotypes, for Tuli Creek flows into Lake Nicaragua near the San Juan. The type specimens are apparently lost. They were supposed to have been sent to the National Museum, but there is no record of their having been received by that institution. It has been pointed out that our specimens differ from the types, but the areolation of the ventral surface may not be a constant feature. *Eleutherodactylus diastema* has been considered by Cope to be closely related to *S. ridens*. I have examined the two types of the former species in the National Museum. The ventral surface of one (U. S. N. M., 25170) is smooth, while that of the other (U. S. N. M., 25171) is slightly areolate.

If *S. ridens* is not closely related to *E. diastema*, it is, at least, very closely allied to the genus *Eleutherodactylus*. If it possessed vomerine teeth, it would be referable to that genus. The digital expansions, although large, are subtriangular in shape and have T-shaped terminal phalanges, as shown in figure 2. The sacral diapophyses are slightly dilated, as in several species of *Eleutherodactylus*. The pectoral girdle is typical of the genus *Eleutherodactylus* (Fig. 1).

10. *Eleutherodactylus ranoides* (Cope)

Lithodytes ranoides COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 275.

Liophyla ranoides COPE, 1893, Proc. Amer. Phil. Soc., XXXI, p. 335. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 225.

Five specimens from the vicinity of Tuli Creek and one from Cukra.

The types of this species (U. S. N. M., 14179) are nearly identical with those (U. S. N. M., 29771-2) of *E. rugulosa* (Cope). The color has faded considerably in these specimens, the gray changing to brown; but *E. rugulosa* may be distinguished from *E. ranoides* by its vomerine teeth, which are in two round fascicles almost touching one another. In the latter species the vomerine teeth are in two transverse fascicles distinctly, although not widely, separated from one another. The former species has the dorsal

surface slightly more tubercular than the latter. In general proportions and in color pattern, the species are very similar. The types of *E. rugulosa* were collected in Tehuantepec, the types of *E. ranoides* in Nicaragua. The former species is not represented in our Nicaraguan collections. It is possible that the two species have been confused in the past and that *E. rugulosa* does not occur in Nicaragua.

The earlier name, *Eleutherodactylus*, is here employed for *Hylodes*. Günther uses the generic name *Liohyla*, but he admits (1900, p. 220) that he retains the name "only because it is convenient to lessen the great number of species described as *Hylodes*."

Two of the specimens of *E. ranoides* from Tuli Creek have a narrow vertebral line of white. All of the specimens have a very fine, longitudinal, white line across the mottled throat region. One very young individual, measuring only 16 mm. from snout to vent, as compared with 43 mm. of the adult, is much browner than the others. In spite of its small size, it has the characteristic mottled throat-patch divided by a white line.

One specimen, an adult male caught November 25 near the edge of Tuli Creek, contained in its stomach a large grasshopper. Fragments of a grasshopper's wing were found in the stomach of another specimen.

11. *Eleutherodactylus polyptychus* (Cope)

Hylodes polyptychus COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 276. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 228, Pl. LXVI, fig. C. DECKERT, 1915, Zoologica, II, No. 1, p. 15.

Twenty specimens, all from eastern Nicaragua and northeastern Costa Rica: Eden Mine, Pia Creek, La Hunter, and Colorado Bar.

In spite of the intensive collecting done in the region of Tuli Creek and the Chontales Mountains, this species was not taken in western Nicaragua. Although apparently limited in range, it displayed considerable diversity in color. The ground tone (in alcohol) is a light tan, but the back is heavily washed with brown. In some of the specimens the dorsal coloration is a uniform brown, but in most of the specimens some of the yellow appears to form indistinct patterns. Two patterns are repeated on several specimens. In one, the yellow appears as two longitudinal stripes, one on each side of the back. In the other, a Λ -shaped yellow mark appears on the pectoral region and a shade of the same on the sacral region.

There is apparently a definite relationship between the size of a specimen and its rugosity. One adult female, measuring 25 mm. from snout to vent, is nearly identical with the types (U. S. N. M., 14180). This specimen

is more rugose than any of the other specimens. Another female of the same size with equally well developed ova is not so rugose as the former, but it is more rugose than the majority of smaller specimens. There is probably some other factor besides maturity influencing the rugosity of this species.

Only a few stomachs were examined. They contained only insects, and mostly large ants. Two adult females were taken with ovaries greatly distended with ova. One was captured October 1 on Colorado Bar and the other October 22 at La Hunter. This would indicate that the breeding season of the species in eastern Nicaragua extends throughout most of October. Specimens were taken in a variety of habitats, but mostly in the dark jungle where undergrowth was thin, due to the absence of sunlight.

12. *Eleutherodactylus rhodopis* (Cope)

Plate XVI, Fig. 1

Lithodytes rhodopis COPE, 1866, Proc. Acad. Nat. Sci. Phila., p. 323.

Hylodes rhodopis GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 232, Pl. LXVII, figs. c and c'. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194. DECKERT, 1915, Zoologica, II, No. 1, p. 15.

One specimen from Kanawa and another from Eden Mine.

E. rhodopis is apparently as variable as other Central American species of *Eleutherodactylus*. But it varies not only in color; there is considerable discrepancy in the leg lengths of the two specimens before me. I have compared these specimens with others from Mexico and Guatemala in the National Museum. The tibio-tarsal articulation in most specimens extends beyond the end of the snout. In one of our specimens it just reaches that point. This specimen is a male with small gonads. The ground color of this specimen was light orange in life, of the other dark brown. The color pattern was nearly the same in both and similar to that described for the species. Both specimens were taken in the dark forest, among the dead, wet leaves on the ground.

13. *Eleutherodactylus rugosus* (Peters)

Hylodes rugosus PETERS, 1873, Monber. Ak. Wiss. Berlin, p. 610. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 233.

Lithodytes megacephalus COPE, 1875, Journ. Acad. Nat. Sci. Phila., VIII, p. 110, Pl. XXIII, fig. 11.

Lithodytes pelviculus COPE, 1877, Proc. Amer. Phil. Soc., XVII, p. 89.

Hylodes megacephalus GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 239.

Thirty-one specimens from several scattered localities: Eden Mine, Backas Creek, Cupitna Camp, Kanawa, Cukra, and Tuli.

This large series of specimens shows conclusively that *E. megacephalus* is but the adult of *E. rugosus*. The specimens range from 8 mm. in length (snout to vent) to 41 mm. The largest specimen is a male; an old female would probably be larger. All of the intermediate steps between the different modes of coloration given for the types of *E. megacephalus* and *E. gulosus* are represented in the series. The incipient stages in the formation of the supraciliary crests characteristic of *E. megacephalus* are found in medium-sized individuals. No specimens from Chiriqui, the type locality of *E. rugosus*, have been available for study, but in the National Museum two specimens (Nos. 29894–29896), probably collected in Costa Rica, and three others (Nos. 29963–29964), from San Carlos, Costa Rica, are identical with young specimens in our series.

Günther was correct in referring *Lithodytes pelvicolus* Cope to *E. megacephalus*. The type (U. S. N. M., 3236) falls well within the range of variation exhibited by young specimens in our series. The tympanum of the type specimen is nearly as large as the eye, but, since the tympanum varies greatly in our series, its size cannot be a diagnostic character.

There is very little external difference between the type of *E. gulosus* Cope (U. S. N. M., 32590) and the type of *E. megacephalus* (U. S. N. M., 32579). Both specimens are females with well developed ova. It is strange that *E. gulosus* is so much larger than *E. megacephalus*. Without other specimens than the type, it is probably best to allow *E. gulosus* to stand as a valid species.

The most striking change in the coloration of *E. rugosus* is the transformation of the dark, purple-brown ground color into a light tan. This change does not take place in adults only. There are many small specimens in the collection which have the coloration described as characteristic of *E. megacephalus*. But the majority of our specimens have the purplish ash coloration characteristic of *E. rugosus*. The most constant features in the coloration of the species are the dark reticulations of the ventral surface, the light interorbital bar, and the dark supratympanic stripe. The dark spots on the back, lips, and legs are generally present, but in very dark individuals most of the color pattern is obscured. In life, the palms and soles of the appendages of the dark individuals are a light tan. This color is retained on the palms in the light variety, but it is generally replaced on the soles by a black.

The majority of specimens were caught in clearings among dead leaves on the ground. These situations were sometimes shady and moist, but never swampy. Only a few stomachs were examined. These contained

mostly beetles. One medium-sized individual contained in its stomach two beetles and a large ant (*Neoponera obscuricornis* Emery). The walls of the stomach of *E. rugosus* are thicker and more muscular than those of any other species of Nicaraguan *Eleutherodactylus* which I have examined.

13. *Eleutherodactylus nubilus* (Günther)

Hylodes nubilus GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 237, Pl. LXIX, fig. a.

Fifty-five specimens from many localities in the east and west; most of the specimens from the vicinity of Tuli and Pia Creeks and from Eden Mine.

Although this species, like *Leptodactylus albilabris*, is common throughout Nicaragua, it has never been taken from that Republic before this time. The species was described only recently from Costa Rica. It is surprising that none of the early collectors found it in Nicaragua.

The species shows such an extraordinary range of color variation that it is easier to point out the few constant characters rather than to try to describe the total range. The gray throat-patch divided by a broad white band, the dark reticulations on the posterior surfaces of the thighs, and the dark interorbital band are more or less distinct in all of the specimens; but in some of the specimens with a broad vertebral line the interorbital bar is indicated only by two spots. The average ground color is not dark purplish, as described for the type, but it is some value of brown. Dark bars on the lips and appendages are often present, although sometimes indicated by only a slight shading. An extensive dorsal color pattern is present in only a few of the smaller specimens. It consists of a dark W-shaped mark on the pectoral region and a dark spot in the middle of the back. A few dark reticulations are sometimes present on the dorsal surface of the snout. Three black spots are occasionally present on each side of the body, one above the tympanum and the other two posterior to it and nearer to the axis of the body. The three dark spots are arranged in an oblique line directed toward the axis. The yellowish vertebral line is present in less than half of the specimens.

Two of the specimens from Maselina Creek have the bodies greatly distended with large ova. One of these specimens was taken September 4, and the other September 13. It seems probable that the species breeds in eastern Nicaragua during the end of September. The species was found in many different habitats, but always in the vicinity of water.

14. **Eleutherodactylus bransfordii** (Cope)

Lithodytes bransfordii COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 274.

Hylodes bransfordii GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 238.

Over a hundred specimens from most of the localities visited in both the east and the west.

E. bransfordii and *E. polyptychus* occur together in the same region. The adults of both species have a number of longitudinal rows of tubercles on the back, and they are very similar in general proportions; but the former species may readily be distinguished from the latter by its narrow snout and different ventral coloration.

Our series of *E. bransfordii* shows a remarkable range of color variation. The ground color is generally some tone of gray or pinkish gray. Numerous darker blotches may appear on the dorsal surface. Of these the most constant are the interorbital band, a Λ -shaped mark on the pectoral region, and a number of cross-bands on the legs. A black spot on the tympanum and another under the eye are almost always present. In the smaller specimens the skin is smooth and the color pattern is not distinct, but a white vertebral stripe is often present.

The digital expansions of *E. bransfordii* are very small and somewhat diamond-shaped. It is generally assumed that the form of the digital expansions and the shape of the terminal phalanges are correlated. We would expect simple phalanges in slightly dilated disks. The terminal phalanges of *E. bransfordii* are T-shaped, but, more strangely still, the phalanges do not extend very far into the small disks. The greater part of the disks are unsupported by bone. If the shape of the terminal phalanges and the form of the digital expansions are correlated, the factor of size must play a considerable rôle.

15. **Bufo hæmatiticus** Cope

Bufo hæmatiticus COPE, 1862, Proc. Acad. Nat. Sci. Phila., p. 157. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 243.

One specimen from Eden Mine.

I have compared this specimen with the type of the species in the National Museum (No. 4344). The type specimen came from Truando, Colombia. In spite of the distance which separates the localities where these two specimens were collected, they are, nevertheless, nearly identical in color as well as in relative proportions.

Our specimen of *Bufo hæmatiticus* was caught among the leaves on the

ground in a dense, but not swampy, jungle. It had been feasting on ants. Its stomach contained a great many large red and black ones. The following species were represented in the contents of this single stomach: *Pachycondyla harpax* F. (4); *Ectatomma ruidum* Rog. (1), *Eciton hamatum* F. (3), *Atta cephalotes* (4), *Apterostigma* sp. (1).

16. *Bufo marinus* (Linné)

Rana marinus LINNÉ, 1758, Syst. Nat., I, p. 356.

Bufo marinus IVES, 1891, Proc. Acad. Nat. Sci. Phila., p. 461. COPE, 1893, Proc. Amer. Phil. Soc., XXXI, p. 335. MOCQUARD, 1899, Bull. Soc. Philom., (9), I, p. 166. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194. ATKINSON, 1907, Ohio Naturalist, VII, p. 151. RUTHVEN, 1912, Zool. Jahrb. (Syst.), XXXII, p. 309.

Over a hundred specimens from several localities in the east and the west; most specimens from the town of Rio Grande.

The range of variation in this large series is very small, and nothing more than has already been described by several authors, most recently by Ruthven (1912, p. 309). The sexually mature males are readily distinguishable from the females by the numerous, low, spiny tubercles on the back. This rugosity is correlated only with sex. It is not to be confused with the rugosity caused by external factors. Such rugosity occurs in several species of *Eleutherodactylus* and *Leptodactylus*; and, as we have shown above, is probably due to the influence of the environment.

A rather varied diet was found in the few stomachs examined. This consisted chiefly of large cockroaches. Such insects were to be expected, since the majority of these giant toads were taken around street lamps in the town of Rio Grande.

17. *Bufo coniferus* Cope

Bufo coniferus COPE, 1862, Proc. Acad. Nat. Sci. Phila., p. 158. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 251, Pl. LXIX, fig. B.

Three specimens from eastern Nicaragua, one from each of the following localities: Cupitna Camp, Kanawa, and Maselina Creek.

The type specimen (U. S. N. M., 4335) of this species was collected in Turbo, Colombia. It is larger than any of our specimens and differs in having more tubercles on the back. These tubercles are less pointed than in our specimens. There is apparently no other difference between our specimens and the type. Our largest specimen measures only 49 mm. from snout to vent. None of the specimens are sexually mature.

In alcohol, these three toads appear nearly uniform gray with a slight indication of a darker pattern; in life, they were very different. The dorsal ground tone was bright leaf-green with velvety dark gray, almost black, markings, tending to form a Λ -shaped mark on the pectoral region and a pair of ocelli on the sacrum. These dark markings were replaced by light gray blotches in one specimen. On the edges of some of the gray blotches there appeared a few large cream-colored spots. In another specimen the hands, feet, upper arms, and anterior part of the femoral regions were all tan-colored. Laterally there was a row of tubercles washed with tan, but the tubercles on the back were the same as the ground tones of the regions in which they were situated. The sides of the head were tan, but appeared metallic green in reflected light. The ventral surface was green, mottled with gray. The pupil of the eye was horizontally elliptical. The iris was golden with a greenish tint and it was reticulated by a few black veins.

The specimens were caught in three different but related habitats:

- 1.) Soft mud on the edge of the rain forest.
- 2.) Moist leaves covering the floor of the forest.
- 3.) Moss-covered vine about five feet from the surface of the water in a forest swamp.

Most of the stomach contents consisted of beetles, but a few ants were present. Several large weevils, a large histerid, and a few ants were contained in one stomach. The ants in this stomach were *Paraponera clanata* F., *Neoponera obscuricornis* Em., *Apterostigma* sp., and *Hylomyrma* sp.

18. *Bufo valliceps* Wiegmann

Bufo valliceps WIEGMANN, 1833, Isis, p. 657. IVES, 1891, Proc. Acad. Nat. Sci. Phila., p. 461. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 252. GADOW, 1905, Proc. Zool. Soc. London, part 2, p. 194. ATKINSON, 1907, Ohio Naturalist, VII, p. 151. RUTHVEN, 1912, Zool. Jahrb. (Syst.), XXXIII, p. 309.

Nearly a hundred specimens; two from Tuli Creek, all of the rest from the east, where they were taken in nearly every locality visited.

Specimens of this species in the National Museum from Guatemala and Costa Rica agree perfectly with our series; but the average condition of the large series of *B. valliceps* in the American Museum from Texas is much more rugose above. The warts are more numerous and flatter in the Texan specimens than in the Nicaraguan specimens. Günther (1900, p. 252) has noted this discrepancy in the northern and southern specimens, and has pointed out that there is a constant difference in color. It is probable that there are

two races of *B. valliceps* in Central America. No specimens from Honduras and Mexico are available for study and it is impossible to determine the ranges of these forms. It is possible, however, that the northern form is but a local variation. There are not sufficient data upon which to base a subspecies.

The color of *B. valliceps* is variable, but, as in many other species of *Bufo*, it follows a definite sequence in its development. In the young, a pattern is present, consisting of three or four black spots on the back, a black interorbital bar, and dark cross-bars on the legs. A light vertebral stripe is nearly always present. As the individual matures, the ground tone becomes much darker and the color pattern gradually disappears. This change in coloration apparently does not always progress evenly. Many of the smaller specimens in the collection do not have the black spotting. In very small specimens the black spots are not present.

B. valliceps was taken in a great variety of habitats. It was often associated in the woods with *B. marinus*, but that species outnumbered it five to one. It was rarely seen about human habitations, but was noted in almost every other place, from the sea beaches to the highest mountains visited.

19. *Hyla chica*, new species

Plate XVIII

Diagnostic characters.—Very small. Vomerine teeth, if present, in two small, widely separated, oblique groups between the choanæ and behind the level of their posterior margins. Fingers free; toes barely webbed, the web very fleshy and hardly distinguishable from the metatarsal region. The following phalanges of the toes free: first (inner) toe, two; second toe, two; third toe, two and two-thirds; fourth toe, three and three-fourths; fifth toe, two and one-third. Tympanum one-third the diameter of the eye. Tibio-tarsal articulation reaching the eye or slightly beyond.

Description of Type (Sexually mature male).—Extremely small; tongue longer than broad, unemarginate behind; vomerine teeth absent; head slightly longer than broad; snout slightly longer than diameter of the eye, sharply pointed, slightly projecting; canthus rostralis distinct; loreal region scarcely concave; interorbital space broader than upper eyelid; tympanum pigmented and not very distinct, about one-third the diameter of the eye. Fingers free; toes slightly webbed, the web very fleshy and hardly distinguishable from the metatarsal region; first (inner toe) with two phalanges free, second toe with two, third toe with two and two-thirds, fourth toe with three and three-fourths, fifth toe with two and one-third; disks of the digits sub-diamond-shaped, smaller than tympanum; subarticular tubercles distinct; one metatarsal tubercle; no tarsal fold; tibio-tarsal articulation extended forward reaches the middle of the eye. Entire upper surface smooth; belly and lower part of throat slightly granular; no folds on dorsal surface; a distinct fold across the chest.

Ground color, in alcohol, light yellow, both dorsal and ventral surfaces tinged with brown, which appears under the lens as a number of widely separated melanophores; a dark brown stripe on each side of the head from the tip of the snout along the canthus rostralis, through the edge of the upper eyelid and fading out upon the tympanum; a broad interorbital bar fading out gradually on its posterior margin; a spot in front of the interorbital bar of the same color; a number of dark mottlings in the middle of the back extending from the pectoral to the sacral regions; posterior surface of thighs, dorsal surface of tibio-fibulas, and forearms tinged with dark brown; two pale stripes across each of the two last-mentioned surfaces; entire ventral surface uniformly stippled with brown.

Color in life nearly the same; the cross-bars on legs and arms yellow; ventral surface slaty yellow; "color of internal organs plainly seen through the delicate skin."

Dimensions.

Tip of snout to vent.....	16.0 mm.
Width of head.....	6.5
Length of fore limb from axilla.....	9.5
Hind limb from vent to tip of longest toe.....	21.5

Type.—A. M. N. H., 8230; near Bluefields, Nicaragua,—Maselina Creek, two miles from mouth; Halter and Mannhardt collectors, June 23, 1916.

There are two other specimens from Maselina Creek in the collection referable to this species. These specimens are not so well preserved as the type. They differ from the latter chiefly in having two groups of vomerine teeth which lie posterior to the choanæ and are obliquely directed backward. The specimens differ somewhat in color from each other. In one, the ventral surface of the legs is dark brown, and the dark head stripe extends slightly posterior to the tympanum. In other ways it is very similar to the type. The other paratype is an adult female. It is much larger than the male, measuring 20 mm. from snout to vent. This specimen is a nearly uniform brown on the back and is lighter below. In life it was different in coloration from the other two specimens. The collectors described it as dark brown above, with a light interorbital bar of grayish brown. The melanophores on the ventral surface were widely separated, giving the throat and belly a stippled appearance. The chest was less spotted than the rest of the ventral surface, and the ground color of that region was bluish white instead of yellowish white. The eyes of all the specimens were very similar. The pupils were black, horizontal, elliptical, but nearly round. The upper half of the iris was a bright tan, the lower half a bronzy brown.

All of the specimens were taken on the swamp-lands bordering the Maselina Creek. The type specimen, to quote directly from the collectors' field notebook, was "caught on the under side of a cocoanut palm leaf after an all-day rain. When approached with a bright acetylene lamp, it did

not become disturbed, but at intervals of eight or nine seconds it would inflate the vocal sack, puff up the body enormously for its size, and then with a snap would 'peep' once. This 'peep' was high-pitched and very loud, like the sudden pulling of a high-strung piano wire."

This male was taken June 23; the adult female was taken September 13. It is very probable that the male was calling for a mate, since its gonads were



Fig. 3.

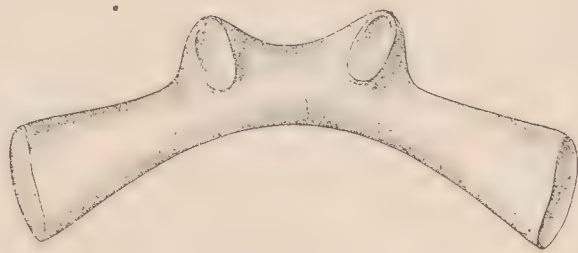


Fig. 4.

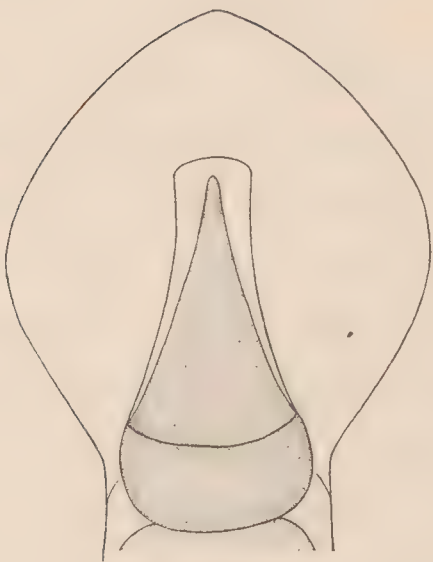


Fig. 5.

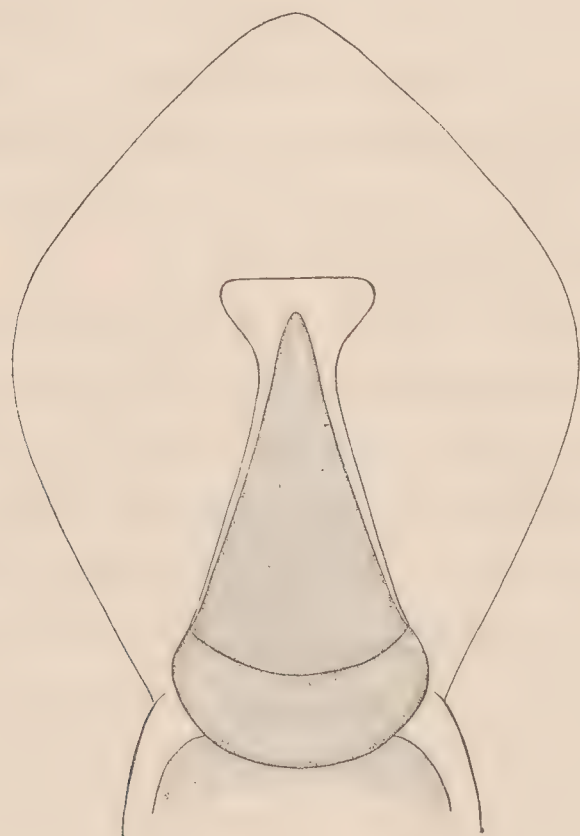


Fig. 6.

Fig. 3. Pectoral girdle of *Hyla chica*, new species.

Fig. 4. Sacral diapophyses of *Hyla chica*, new species.

Fig. 5. Terminal phalanx of finger of *Hyla chica*, new species.

Fig. 6. Terminal phalanx of toe of *Hyla chica*, new species.

very well developed. The breeding season of the species may be prolonged through several months; but on this point we can only conjecture. The smallest specimen was caught September 13 "on the upper surface of a large leaf in a swamp." It seems probable that the species, at least during the breeding season, is confined to the swamp-lands.

Hyla chica may be readily distinguished from any other *Hyla* by its remarkably short webs and small size. The type specimen, although only

sixteen millimeters in length, possesses well developed gonads. This specimen has a superficial resemblance to an adult *Syrrhophus ridens*, with which it agrees in general form, color, and in the absence of vomerine teeth. But the shape of the digital expansions and the length of the toes at once distinguishes the two species. The close relationship of *Syrrhophus ridens* to *Eleutherodactylus* has been discussed above. The digital expansions are very similar to those of that genus, while in *chica* they are diamond-shaped, as in several other species of *Hyla*.

The terminal phalanges of *H. chica*, in spite of their small size, are claw-shaped. In the male, the majority of phalanges are typically claw-shaped, but several of the phalanges of the female show a slight dilation. The extreme range of this variation in phalanx form is shown in figures 5 and 6. It is interesting to speculate how these dilations arose. The claw-shaped phalanges of most hylids show little variation. *H. chica* resembles several species of *Eleutherodactylus* in the shortness of its web. That genus is characterized in part by T-shaped terminal phalanges. Does the reduction of the web cause new mechanical strains to be evolved? Are these dilations a response to such strains? Too little is known about the habits of this tiny tree-toad to warrant any conclusion as to the origin of the phalanx dilations.

Other structures than the phalanges are modified in this species. *H. chica* shows many signs of degeneracy, or at least of specialization on a simpler plan than that found in most of the species of *Hyla*. Its pectoral girdle is weak, the sternum being very narrow (Fig. 3). The sacral diapophyses are very slightly dilated, as shown in figure 4. This condition may be due to the small size of the species, for in other hylids of small size, such as *Pseudacris* and *Acris*, the sacral diapophyses are nearly cylindrical. In *Hyla crucifer* the sacral diapophyses are more dilated than in *Hyla chica*, but the former species is much the larger. The modern tendency in the classification of the larger groups is to regard the shape of the sacral diapophyses of great diagnostic importance. *Syrrhophus ridens* has these structures longer and slightly more dilated than *Hyla chica*. Yet we refer the former species to the Leptodactylidæ, and the latter to the Hylidæ. We do this because the sum total of the internal structures of *Syrrhophus ridens* points toward *Eleutherodactylus* as the stock from which that species arose, while the internal structures of *H. chica* are modified, but show distinctly their *Hyla* origin. There is no use of referring *H. chica* to any other genus than *Hyla*. It has been shown by Günther (1900, Biol. Centr.-Amer., Batr., p. 286), Gadow (1901, 'Amphibia and Reptiles,' p. 203) and more recently by von Kampen (1906, 'Resultats de l'Expedition Scientifique Néerlandaise à Nouvelle-Guinée, Amphibia,' p. 174) that the genus *Hylella*

is very artificial. It is probable that *H. chica*, with its small size and weak or absent vomerine teeth, holds the same position in the amphibian fauna of Nicaragua that *Hyla smithii* does in Mexico.

20. *Hyla boulengeri* (Cope)

Plate XVII

Scytopsis boulengeri COPE, 1887, Bull. U. S. Nat. Mus., XXXII, p. 12.

Hyla boulengeri GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 267.

Three specimens, one from each of the following localities: Kanawa, Sioux Plantation on the Rio Grande, and Tuli Creek.

Hyla boulengeri was hitherto known only from the type, which is now in the National Museum (No. 13974). This type specimen is smaller than two of our specimens and larger than the third. It differs considerably from its original description, which reads in part:

Eye prominent, size moderate; its diameter twice that of tympanic membrane, and equal interorbital width, and the length from its anterior border to the nostril. . . . Fingers free, the first opposing the second, which is longer and equal to the fourth (fifth).

The most striking feature of *Hyla boulengeri* is its long, depressed snout. In our specimens the distance from the eye to the nostril averages one and one-third times the greatest diameter of the eye. In the type specimen this distance is one and one-fourth times the greatest diameter of the eye, and not equal to the orbit's diameter, as stated by Cope. Moreover, the tympanum is nearly two-thirds the diameter of the eye in the type specimen. The second finger is distinctly shorter than the fourth in all of the specimens. Cope placed the species in the genus *Scytopsis*, which was characterized by an accumulation of sebaceous glands above the tympanum, but these glands are not prominent in any of the specimens. Only a slight indication of a supratympanic fold is present.

Our specimens in life differed from each other in the intensity of their coloration, but their color pattern was much the same. The lightest colored specimen was an adult female and in life the ground tone above was an ash gray, tinged with yellow. A metallic bronze-like lustre was visible in certain lights. When the leg was contracted into the resting position, the exposed parts were the same color as the back. The concealed parts were dark lemon yellow and were crossed by three black bars which tended to form regular transverse stripes across the legs when they were slightly extended. The sides of the abdomen were yellowish green, spotted with

black. The throat region was mottled with white and brown, the reticulations fading out on the belly. The ventral surface of the legs was yellowish, mottled with gray. The three black bars on the femoral and tibial region were visible from below. When the pupil was contracted, the iris appeared a light bronze and it was divided into quarters by a series of black lines.

The other two specimens of the series were much darker in life than this female, but the metallic lustre was present. In alcohol the yellows have faded and the specimens are tinged with a purple of low intensity.

Two of the specimens were caught in the immediate vicinity of sluggish streams; the third was found among the wet leaves covering the floor of the forest about Kanawa. This specimen was taken August 16. It was a female with ovaries greatly distended with ova. This would indicate that the breeding season of *H. Boulengeri* occurs about the end of August. Food was found in the stomach of one specimen. The remains of three grasshoppers were distinguishable.

22. *Hyla quinquevittata* Cope

Hyla quinque-vittata COPE, 1886, Proc. Amer. Phil. Soc., XXIII, p. 273. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 268. ATKINSON, 1907, Ohio Naturalist, VII, p. 152.

Two half-grown specimens from Tuli Creek and one adult from Cukra.

The type of *Hyla quinquevittata* is now in very poor condition and probably was in little better shape when Cope made his description, for our fresh specimens do not correspond entirely with the original description. The type specimen (U. S. N. M., 14187) was probably placed in too strong alcohol, for it is very badly shrivelled. The fingers appear to have a slight rudiment of a web, but this may be due to shrinkage, for in two of our specimens there is no trace of a web. When the body of the type specimen is straightened out, the tibio-tarsal articulation marks the end of the snout, or at least does not extend beyond that point, as stated by Cope.

There is a great discrepancy in the published description of the closely related *Hyla phæota*. Günther (1900, p. 269) has remarked upon this point. The type specimen of the species is in the National Museum. The three outer fingers are slightly webbed. The tympanum is three-fourths the size of the eye. Nearly three phalanges of the fourth toe are free, the rest of the toes are webbed to a point half the length of the penultimate phalanges.

Our specimens of *Hyla quinquevittata* range from 16 mm. to 32 mm. in length. In color they differ chiefly from one another in the distinctness of

the dark longitudinal bands. In the two smaller specimens the dark bands are broken up, only one band on each side of the back being sharply defined. In the largest specimen only a few dark reticulations indicate the position of the bands. The characteristic bars on the legs occur in only the smallest specimen, but a few dark blotches are present on the legs of the other specimens.

The habitat of *Hyla quinquevittata* is apparently the dense jungle. Two of the specimens were caught among the leaves on the ground. The third was bought from a native. The largest specimen contained in its stomach over a dozen termites and one ant (*Tetramorium quineense* Fabr.).

23. *Hyla baudinii* Duméril and Bibron

Hyla baudinii DUMÉRIL AND BIBRON, 1841, *Erpét. Gén.*, VIII, p. 564. WERNER, 1896, *Verh. Ges. Wien*, XLVI, p. 350. GÜNTHER, 1900, *Biol. Centr.-Amer.*, *Batr.*, p. 270, Pl. LXXI. GADOW, 1895, *Proc. Zool. Soc. London*, part 2, p. 194. RUTHVEN, 1912, *Zool. Jahrb. (Syst.)*, XXXII, p. 310.
Smilisca baudinii DECKERT, 1915, *Zoologica*, II, No. 1, p. 12.

Fifteen specimens from the Sioux Plantation and twelve from Cooley Plantation, on the Río Grande; three specimens from Cukra.

Ruthven (1912, p. 310) has recently described the colors of this variable tree-toad in life. The majority of our specimens have the ground color of the back some tone of brown, but other specimens show the complete range of variation discussed by Ruthven. Specimens from Mexico in the National Museum and in this Museum, are in no way different from our Nicaraguan specimens. Three specimens (A. M. N. H., 3984-3986) from Colombia, collected by H. G. F. Spurrell, and presented to the American Museum by the British Museum, do not differ from the Nicaraguan specimens in color, but they may, nevertheless, be a distinct geographic race of *H. baudinii*. The hind legs are longer than in any of our specimens, the fingers and toes are somewhat thicker. The sternum is wider than in any of the five Nicaraguan specimens I have examined. There are other less important differences. No specimens of *H. baudinii* from Costa Rica or Panama are available for study. There may be specimens showing intergrading characters in these regions. Without a larger series of specimens, it does not seem advisable to describe this race.

The males of *H. baudinii* differ from the females in possessing two external vocal pouches, but there are other differences by which the sexes may readily be distinguished. The females are much larger than the males. Their tibio-tarsal articulation extends further forward, and their tympanums are relatively larger.

Five females with the ovaries distended with ova were collected on the Rio Grande between July 15 and July 25. This places the breeding season of *H. baudinii* in the region of the Rio Grande about the end of July. The vast majority of the specimens of *H. baudinii* were taken in the damp roof-thatching of native huts. The collectors made several of these huts their headquarters and sometimes they had only to step out of their door to collect a number of specimens under the eaves. Only a few of the stomachs examined contained food. This consisted entirely of grasshoppers.

24. *Hyla albomarginata* Spix

Hyla albomarginata SPIX, 1824, Nov. Spec. Test. Ran., p. 33, Pl. VIII, fig. 1.
GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 284.

Two specimens from Maselina Creek.

No specimens in the collection have changed so completely in color upon being placed in alcohol as have these two specimens. *H. albomarginata* is usually described as yellowish or pinkish above, uniform or minutely spotted with purple; ventral and lateral surfaces whitish. In alcohol, our specimens agree perfectly with this description; but in life the specimens were differently colored. One specimen, caught near the Maselina Creek on some shrubbery about a foot from the ground, was generally green above. The ground tone was yellowish green between the girdles. This region was minutely spotted with white and brown, which in certain lights appeared very much like frost. The throat region was a light bluish color, the belly a lemon yellow. The appendages were especially brilliant in color. The upper arm was a bluish green, the lower arm a pale green. The hands were lemon yellow. The legs were generally bluish green, but the feet, like the hands, were yellow. The webbing between the toes was bright reddish orange, in strong contrast to the yellow of the toes.

The other specimen was found crouched on a log floating in the Maselina Creek. The log was in the shade of the overhanging limbs of trees. As in the other specimen, the ground tone of the back was green, but along each side of the back there was a stripe of yellowish gray extending from the eye to the groin. The nostril region was tinged with brown, the throat with blue-green. The rest of the ventral surface was uniform yellowish white. After capture, and while still alive, this specimen changed its entire coloration. The ground tone of the back became lemon yellow, with a diffusion of brownish spots between the dorso-lateral stripes. The end of the snout became dark brownish yellow and two or three spots of the same color appeared on the back. The dorso-lateral stripes changed to light yellow

and were edged faintly with orange. A few shades of brownish yellow appeared on the appendages. The webs of the feet remained orange, but the color was of less intensity than before. The ventral surface remained yellowish white, but the blue-green faded from the throat region.

This specimen, which was caught on a log, had recently eaten one small beetle, one grasshopper, and a very large ichneumon wasp. This wasp had a very long ovipositor. The abdomen of the wasp was removed from the small intestine of the frog, but the end of the ovipositor, still connected with the abdomen, was found in the œsophagus. It does not seem that this frog could have had a very enjoyable meal.

The other specimen of *H. albomarginata* was a female with very large ovaries. This specimen was caught August 16. It is probable that the breeding season of the species in the vicinity of the Maselina Creek occurs about the end of August.

25. *Agalychnis helenæ* Cope

Plate XVI, Fig. 2

Agalychnis helenæ COPE, 1884, Proc. Amer. Phil. Soc., p. 182. GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 290.

One specimen from Cukra region and another from Colorado Bar, Costa Rica.

The latter specimen was kept in an observation cage and studied by Mr. Halter. The following notes are from his field note-book. The specimen was caught at 12 o'clock noon on the upper side of a leaf of a banana tree standing near the edge of the jungle. / During captivity, the dorsal coloration was subject to considerable variation. Generally the ground tone was a dark slaty green or a bright leaf-green. A number of pale green spots would often appear. These did not seem to be dependent upon the intensity of the light. They appeared irregularly scattered over the back. Sometimes they would form an H-shaped mark just anterior to the pectoral girdle. The changes in the color of the ground tone did not seem to be correlated with changes in the lighting. The concealed portions of the legs, which appear purplish in alcohol, were a deep blue in life. The feet and hands were brilliant orange. The edge of the upper eyelid was a deep yellow, in striking contrast to the orange-red iris. The ventral surface of the throat and body was yellowish white, of the anterior appendages a slaty color, of the posterior appendages a yellowish white washed entirely, except for a narrow strip, with the deep blue of the concealed portions.

The specimen was rather awkward in its movements. Before jumping,

it would crouch on all fours with appendages at right angles to the axis of the body. It would then laboriously raise the body about an inch from the ground. It would remain in that position for a few seconds, studying the nearby objects, and then would suddenly leap toward one. This specimen could not be induced to feed in captivity. It was tempted with a great variety of food during both the day and evening.

The other specimen was taken at Cukra by a resident sometime during the month of August. It is a female with ovaries distended with ova. This would tend to show that the breeding season of *Agalychnis helenæ* in eastern Nicaragua is about the end of August. Two additional specimens were observed at San Miguel. They were found hiding under the eaves of a native hut. The species is probably wide-spread throughout Nicaragua, for it is known everywhere as "la rana de los platanos."

26. *Œdipus striatulus*, new species

Plate XIX

Diagnostic characters.—Habit similar to *O. variegatus*, but slightly more slender; fingers and toes short, completely enveloped in a web; thirteen costal grooves; distance from snout to vent four times or slightly less the distance to gular fold; parasphenoid teeth distinctly separated from the palatine teeth; ventral surface light yellowish brown, finely streaked with many dark brown lines.

Range.—Nicaragua and Costa Rica.

Type.—Cat. No. 6999, A. M. N. H.; Cukra, Eastern Nicaragua, Halter and Mannhardt collectors; Aug. 2, 1916.

Description of Type.—Palatine teeth in two arched series extending outward beyond the choanæ, and separated from the parasphenoid teeth by a distinct interval; parasphenoid teeth forming a single patch. Head slightly wider than body, truncate; greatest diameter of the eye slightly shorter than distance of anterior corner from the nostril; angle of mouth under posterior edge of the eye; nostril small. Body elongate, not stout; distance of snout from gular fold contained in the distance of gular fold from the anterior edge of vent slightly less than three times; legs short, not meeting on the sides of the body by a distance less than the length of the fore leg. Fingers and toes short, completely enveloped by a web. Tail cylindrical; the distance from the posterior edge of vent to tip of tail equal to distance from the former point to the corner of the mouth; skin smooth; a distinct gular fold; thirteen costal grooves, including the ones in the axilla and groin.

Ground color (in alcohol), both above and below, a pale yellowish tan of low intensity; top of head finely marked with a number of dark brown streaks which radiate from the upper eyelid and assume a longitudinal direction; nuchal region finely streaked with these fine, thread-like lines; on each side of the back a broad streak of dark brown; space between these stripes streaked with fine markings similar to those of the neck region; on the outside of these stripes a number of fine specks of dark brown; sides of the head and body covered above by a stripe of dark

brown and below by a number of fine streaks of the same color; ventral surface streaked by many fine lines of brown; a broad stripe in the mid-line extending from the gular fold to part way the length of the tail; appendages heavily streaked with brown.

Dimensions.

Tip of snout to gular fold.....	11.5 mm.
Tip of snout to vent.....	41.5
Tip of snout to tip of tail.....	85.0
Axilla to groin.....	24.0
Fore leg.....	8.5
Hind leg.....	9.5

Besides the type there have been available for study three other specimens which are referable to this species. One of these was collected in the Chontales Mountains by a native and donated to the collectors. Another was taken on Mt. Mombacho by Mr. W. De W. Miller of the American Museum's ornithological expedition. The third was collected on Mt. Turrialba, Costa Rica, in 1906 by J. F. Tristan and C. F. Underwood. It is now in the National Museum.

The largest specimen of the series was taken in the Chontales Mountains. It agrees with the Costa Rican specimen in having a slightly longer body than the type. In this large specimen the distance from snout to gular fold is contained in the distance from the gular fold to vent exactly three times. The dorsal coloration of this specimen is somewhat different from the type. The fine streaks are mostly replaced by stipple marks, and most of the fine spots between the dorsal and lateral stripes are absent. The ventral streaking of all the specimens, however, is nearly the same and apparently forms a good specific character.

O. striatulus is closely related to *O. variegatus*, but may be distinguished from that species by (1) its shorter body, (2) its very different coloration, especially of the ventral surface, and (3) its slightly different arrangement of teeth. It is also apparently related to *O. dofleini* (Werner), but that species was described as much more robust than *O. variegatus*. Our specimens of *O. striatulus* are decidedly more slender than specimens of *O. variegatus* from Mexico in the Museum of Comparative Zoology, the National Museum, and the Philadelphia Academy of Natural Sciences. Furthermore, our specimens have a very different coloration from that described for *O. dofleini*.

I feel justified in retaining the genus *Ædipus*. In this I have followed the recent work of Fowler and Dunn (1917, Proc. Acad. Nat. Sci., LXIX, p. 21). There is no transitional species between *Ædipus* and *Eurycea*. It seems to me that the several species of *Ædipus* form a natural group.

Although the four specimens of *O. striatulus* were taken in four widely separated localities, situated at different altitudes ranging from sea-level to at least 3500 feet, still these specimens are surprisingly similar and are very different, at least in color, from any previously described Central American salamander. *O. striatulus* is not a local form, but a wide-ranging species. Future work may show that it entirely replaces *O. variegatus* in Nicaragua and Costa Rica. There are one or two records of *O. variegatus* from Costa Rica which I have not been able to confirm, but there is no definite record of *O. variegatus* having been taken in Nicaragua.

The type specimen was found near Cukra under a fallen fence among dead, yellowish leaves which were strewn along a path leading to a deserted plantation. The coloration in life of this specimen was practically the same as that described above for the preserved specimen. The brown and tan color pattern made the salamander very inconspicuous as it wriggled among the leaves. In walking, this specimen raised the body from the ground, the tip of the tail barely touching the surface. When the specimen was put, while alive, in 30% alcohol, it immediately constricted off its tail at a point near the base.

The specimen collected on Mt. Mombacho by Mr. Miller was found on a leaf of a tree about six feet above the ground. It is interesting to find this species having both arboreal and terrestrial habits.

27. *Gymnopsis proxima* (Cope)

Siphonops proximus COPE, 1877, Proc. Amer. Philos. Soc., XVII, p. 90.
Gymnopsis proxima, GÜNTHER, 1900, Biol. Centr.-Amer., Batr., p. 308.

Four specimens, one from each of the following localities: Isle of Boquete on Lake Nicaragua, Hacienda Valencia in the Chontales Mountains, El Bluffs (near Bluefields), and Eden Mine.

The Gymnophiona have recently been revised by Nieden (1913, 'Die Gymnophiona,' Das Tierreich, Berlin). Our specimens agree most closely with *Gymnopsis proxima*, but they do not correspond exactly with Nieden's description of that species. The number of complete annuli varies in the following way: 132 (Bluefields), 135 (Boquete Island), 136 (Chontales Mountains), and 138 (Eden Mine). In all of the specimens the greatest diameter is contained in the body length less than twenty-six times. Two of the specimens are not well preserved and the proportions may be slightly different in life.

Two of the specimens were caught personally by the collectors. One was found at dusk near a very muddy but only temporary swamp. The

color above was very dark gray. The ventral surface at the extreme anterior and posterior ends was the same color, the rest light gray. The other specimen was taken in the afternoon just after a shower. The place where it was found was not at all swampy. This specimen was colored in life like the other one.

EXPLANATION OF PLATES

PLATE XIV

Figure 1. *Rana palmipes* Spix.

Figure 2. Rio Grande, Nicaragua, showing the open river banks where *Rana palmipes* was often found.

PLATE XV

Figure 1. *Rana austricola* (Cope).

Figure 2. *Leptodactylus pentadactylus* (Laurenti).

PLATE XVI

Figure 1. *Eleutherodactylus rhodopsis* (Cope).

Figure 2. *Agalychnis helenæ* Cope.

PLATE XVII

Figure 1. *Hyla boulengeri* (Cope).

Figure 2. Woods near Cukra showing habitat of *Hyla boulengeri*.

PLATE XVIII

Hyla chica, new species.

PLATE XIX

Ædipus striatulus, new species.



Fig. 1. *Rana palmipes* Spix



Fig. 2. Rio Grande, Nicaragua, showing the open river banks where *Rana palmipes* was often found



Fig. 1. *Rana austriaca* (Cope)



Fig. 2. *Leptodactylus pentadactylus* (Laurenti)



Fig. 1. *Eleutherodactylus rhodopis* (Cope)



Fig. 2. *Agalychnis helena* Cope



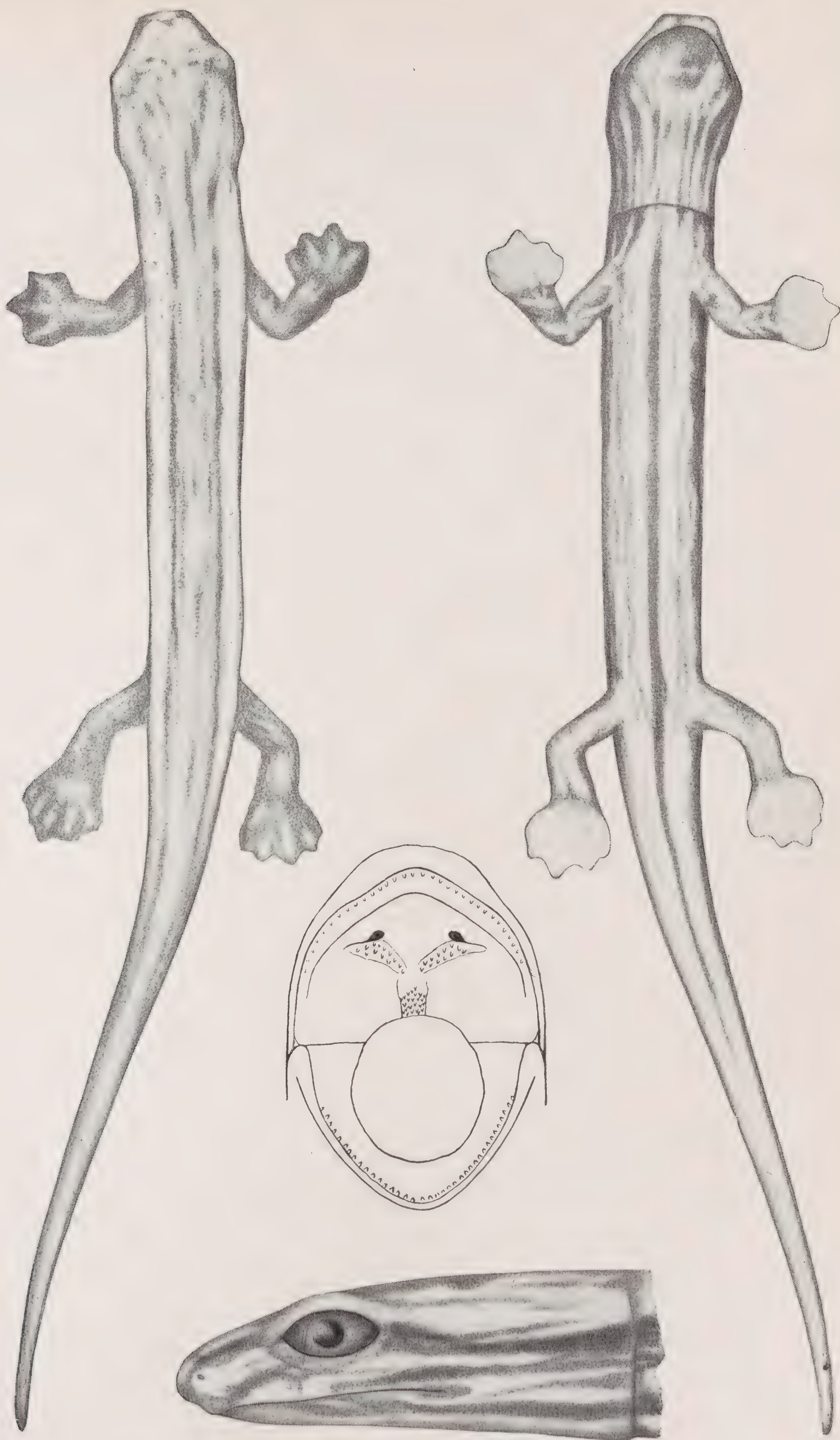
Fig. 1. *Hyla boulengeri* (Cope)



Fig. 2. Woods near Cukra showing habitat of *Hyla boulengeri*



Hyla chica, new species



Edipus striatulus, new species

Article XI.—THE SKULL OF *ZIPHIUS CAVIROSTRIS*

BY JOHN D. KERNAN

PLATES XX TO XXXII

For the opportunity of making this study of the skull of *Ziphius*, I am indebted to the authorities of The American Museum of Natural History. My heartfelt thanks are due also to Professor H. von W. Schulte, of the Department of Anatomy of Columbia University, for much valuable advice and assistance.

As is known, Cuvier was the first to describe the skull of this animal, to which he gave the name of *Ziphius cavirostris*. At the time, he was under the impression that he was describing a fossil skull. This error was later corrected by Gervais, who, in 1850, identified a fresh skull, found that year, as of the same species as the original type specimen. Since that time numerous descriptions have been published by European, American, and Australian observers. The skulls serving as material for the various papers have been assigned to nearly as many species as they number. The tendency, as the material became better known, has been to reduce the number of species. European authorities early agreed that there was but one. True, writing in 1910 with a large amount of material at his disposal, came to the same conclusion. According to him, the differences found in the several specimens were only such as could be accounted for by the variations in age and sex. The question of species, therefore, will not be touched upon by me.

The two skulls in my possession, one disarticulated, lend themselves especially to a study of the individual bones, the character of their articulations, and their relations to the cranial cavity.

Accordingly, I shall endeavor to take up, for the most part, only these points. Comparisons with skulls elsewhere described will not be made although the literature will be cited as far as possible, enabling anyone interested to make them for himself.

The smaller of the two skulls, American Museum Collection No. 80016, is that of a foetus at term, sex unknown. Its measurements are given in the table with those of the older skull. It is easily disarticulated, allowing study of each bone by itself.

The older skull, American Museum Collection No. 80015, is that of a young adult female. As we should expect, it possesses those marks given

by True as distinguishing the female skull namely: small prenarial depression and slight mesirostral ossification.

Table of Measurements

	Large	Small
Total length of skull	854 mm.	435 mm.
Length of rostrum	475	215
Height from vertex to inferior border of pterygoids	420	200
Length from tip of rostrum to post border of pterygoids	680	310
Length from tip of rostrum to anterior end of nasals	655	300
Breadth between centers of orbits	440	200
Breadth between zygomas	462	240
Breadth between temporal fossæ	275	
Breadth of rostrum at base	290	90
Breadth of rostrum at middle	108	49
Breadth of premaxillæ at middle of same	57	24
Depth of rostrum at middle	66	24
Breadth of premaxillæ at front of nares	157	67
Greatest breadth of anterior nares	62	27
Length of temporal fossæ	130	
Breadth of temporal fossæ	70	
Length of orbit	110	64
Length from anterior end of orbit to maxillary notch	85	35
Length of tympanic bulla	53	50
Breadth of tympanic bulla	40	40
Length of mandible		36.5
Length of symphysis		75
Depth of mandible at coronoid		75

NORMA VERTICALIS

We may conveniently accept the two regions usually described in connection with this skull, the rostral and the cranial.

Three areas can be distinguished on the dorsum of the rostrum: a central depressed area, the mesorostral gutter, flanked on either side by elevations which taper distally.

The mesorostral gutter extends the full length of the rostrum. Its distal one-third is made up entirely by the premaxillæ. These bones meet mesally at the depth of the floor in a linear suture. They spread laterad on either side, and then extend dorsad to form the concave walls of the groove ending above in sharp overhanging margins. At the junction of the distal and mesal thirds of the rostrum, the vomer appears in the floor of the mesorostral gutter, thrusting a sharp apex between the premaxillæ. From this point caudad, the vomer takes up an increasingly extensive area in the

floor of the groove and eventually gains a position in the walls. It articulates on each side with the corresponding premaxilla, the surfaces of the bones passing smoothly into one another. This articulation between vomer and premaxillæ has its caudal limit at the premaxillary foramina. From this point to the mesethmoid, which limits the groove caudally, slender processes of the maxillæ appear in the wall between the vomer and the premaxillæ.

The floor, then, of the mesorostral gutter is made up distally by the premaxillæ, proximally by the vomer. The walls are formed distally by the premaxillæ, proximally by the maxillæ and vomer.

It has been mentioned above that the dorsal margins of the mesorostral groove are formed by sharp, overhanging edges of the premaxillæ. These are practically parallel from the tip of the rostrum as far caudad as the premaxillary foramina. Thence caudad the right premaxilla expands mesad to the extent that its border crosses the midline and closely approaches the left bone. From this point the two continue their course toward the nasal cavities, still having a sinistral inclination. In this region the mesorostral groove is roofed in, chiefly by the right premaxilla. It should be particularly noted that the mesethmoid does not rise to the level of the premaxillæ. Therefore, in the absence of the cartilage the nares communicate freely with one another and the mesorostral groove dorsorostrad to the mesethmoid. This condition is considerably altered in the adult skull.

The lateral elevated regions of this surface of the rostrum are constituted entirely by the maxillæ and premaxillæ. At its extremity and thence a short distance caudad only, the premaxillæ appear. The maxillæ then join them on each side and eventually make up the greater part of the surface, since they grow broader approaching the base; whereas the premaxillæ retain a nearly uniform breadth. The broad base of the rostrum is due to the great lateral expansion of the maxillæ. Between maxilla and premaxilla is formed a linear suture which lies at the bottom of a shallow concavity originating in the reciprocal inclination of the dorsal surfaces of the two bones. This groove leads caudad to a large maxillary foramen which transmits vessels and branches of the fifth cranial nerve. It then expands, to become continuous with the great facial fossa.

The borders of this region are both well-marked. The mesal corresponds to that sharp margin of the premaxilla which overhangs the mesorostral gutter. The lateral is excavated its whole length by an alveolar gutter, which is continuous from premaxilla to maxilla. As the maxilla begins to expand it shows on its margin a prominence, called the maxillary tuberosity, rostrad to which is a depression, the antorbital notch.

Inspection of the adult skull shows in this region a number of marked

differences from the foetal. The component bones are, as might be expected, already synostosed, though the sutures are not yet wholly obliterated. The rostrum shows a more elegant outline, tapering more gradually from base to apex. This may be the effect of a loss in the foetal skull of a certain amount of the tips of the premaxillæ which are not perfect. On the other hand, the rostrum may show, in its shorter and heavier appearance, the effect of sex, as this is characteristic of the male as contrasted with the female, assuming the foetal skull to be that of a male. In the adult, the maxillary tuberosities are more prominent, the antorbital notches deeper, and the antorbital expansion more marked.

The bottom of the mesorostral gutter is occupied by a fusiform crest of bone which has its distal limit at the extremity of the vomer and reaches caudad almost to the mesethmoid. Each extremity is a low, sharp ridge which rises out of the surface of the vomer. In the middle of its course the process forms a broad mass which attains almost the level of the premaxillæ. At the sides it nowhere extends beyond the limits of the vomer and it appears to have no relation to any other bone, so that, as far as the mesorostral ossification in this skull is concerned, it has come from the vomer, not from the mesethmoid (Berardius), nor the premaxillæ (Forbes), nor the prefrontals (Owen).

In skulls of adult males of *Ziphius* the mesethmoid ossification is much more extensive than in this female. It fills the mesorostral groove from the tip almost to the base, rendering the rostrum very massive and powerful.

The cranial portion of the skull is quadrilateral in form. Its rostral limit is the line already mentioned. Its caudal limit is at the foramen magnum. It is bisected by the great transverse crest of the skull.

Rostral to the transverse crest we may describe a mesal and two lateral areas.

The mesal region is somewhat elevated, as a whole, and markedly so at its lateral margins. Passing caudad, it rises to an almost vertical position. On each side is the expanded dorsal surface of the premaxilla, that of the right much broader. The left is completely occupied by a longitudinal groove, missing in the right bone and its lateral margin is elevated to such an extent as to cause the surface to be almost vertical. Between these two surfaces is a large, single, narial opening, deep in the recesses of which can be seen the rough dorsal border of the mesethmoid. The narial opening is overhung caudad by the apices of the conjoined nasal bones, together forming a triangular pyramid which, morticed between the summits of the premaxillæ, rests its base against the frontals. The smooth triangular dorsal surface of the two nasal bones forms the summit of the skull.

The lateral areas are occupied by the great facial fossæ made up exclu-

sively of the dorsal surfaces of the maxillæ. The lateral limits are the borders of the maxillæ. The mesal limits are afforded by the premaxillæ, which here rise to a higher level, and by the facial crests of the maxillæ themselves, which appear near the dorsal tip of the fossæ. These areas are deeply concave in both transverse and longitudinal extensions, the concavity being more marked in the adult. Rostrally, there is a broad ridge which runs rostrocaudad from the maxillary prominence. A large canal, which joins the infraorbital system, opens near the center. Mesal to the maxillary prominence, the large infraorbital canal has its opening.

Comparison shows that these regions of the central elevated section in the cranium are much the same in the two skulls, though slight differences may be noted. The facial fossa, owing to the greater prominence of the maxillary tuberosities and the thickening of the bodies of the premaxillæ, are much deeper in the adult. Also, the transverse ridge occupies a more vertical position, since the maxillæ and the premaxillæ turn dorsad more sharply. In this, the foetal skull resembles other odontocetes, such as *Mesoplodon*, and the adult skull is more specialized. In the transverse ridge itself the suture between frontals and supraoccipital is obliterated with advance in age. That between the maxilla and frontals still persists. The nasals present a quadrilateral rather than a triangular outline on their upper aspect, the portion overhanging the nares being less sharply angulated. Caudad to the transverse crest, there are no changes to be noted except the closure of the fontanelles.

The mesethmoid ossification in the older animal has extended rostrad to the level of the maxillary foramina where it fills the mesorostral groove, appearing in the gap between the premaxillæ. Thus there is no communication of the nares and mesorostral groove, as found in the younger skull. From this extremity of the mesethmoid there is continued caudad a sharp crest of bone which rises to a thickened protuberance at the rostral border of the nares. Thence a sharp concave margin, the upper edge of the septum, sweeps ventrad, then dorsad, to reach the salient suture of the nasal bones, which forms with it a continuous line. The whole sharp ridge, from the point where it leaves the mesethmoid to its junction with the internasal crest, appears to be formed by a growth dorsad and rostrad of the lateral wings of the mesethmoid, which are designated "ectethmoids" in the description of that bone. It is to be noted that the septum gains sufficient height by the formation of this ridge to completely separate the bony nostrils.

The great transverse crest of the skull has for its main support the continuous line of the frontals, which extend dorsad from their orbital processes to meet in the midline. This central core is reinforced both rostrally and caudally. On the rostral aspect, the maxillæ extend as a thin border almost

to the midline. Between them, the right premaxilla and the solid buttress of the nasals rest against the frontals. The caudal support is afforded by the parietals at the sides and the supraoccipital mesally. In all probability, the parietals extend much closer to the midline than the disarticulated bones indicate. The mesal part of the parietals, however, adheres rather to the supraoccipital than to the parietals and can hardly be separated therefrom.

The significance of the differences between the foetal and the adult skull lies in this, that the most marked peculiarities appear to be postnatal effects. Thus the deep interlocking between the maxillæ and the frontals, which serves to secure the rostrum to the cranium, becomes much more marked with age. Moreover, the transverse crest, which may be conceived of as the result of the pressure of the vertebral column overcoming the resistance of the water as the animal swims, is very much more prominent in the adult, showing that this resistance acts after birth to compress the skull caudo-rostrally.

NORMA BASALIS

The distal extremity of the rostrum is made up entirely by the premaxillæ. They articulate with one another in the midline, and are limited laterad by the oblique maxillo-premaxillary sutures. Caudad, they separate to allow a slender process of the vomer to appear and the caudal termination of each is a pointed projection which lies between vomer mesad and maxilla laterad. The slender surface of the vomer, which appears between the premaxillæ, is continued caudad between the maxillæ till shut off by the meeting of those bones in the midline.

The maxillæ appear extensively in this region. They reach toward the tip of the rostrum pointed extensions which between them enclose the premaxillæ. Thence their surface broadens until they spread the whole breadth of the rostrum. Caudad to this area, they are overlain by the palate bones, which in turn support the pterygoids. The mesal borders take an oblique course toward the midline, resting successively on premaxillæ, vomer, and opposite maxillæ. At the caudal extremity of the intermaxillary suture, a small area of the vomer appears.

The lateral borders of the maxillæ establish the margins of the rostrum and have already been described. Beneath each maxillary tuberosity a shallow canal gives passage to the facial nerve. The surfaces of each premaxilla and maxilla are marked by a continuous furrow which deepens caudad and finally disappears beneath the overlying palate bone. This furrow marks the course of the posterior palatine canal.

The palate bones present, at the base of the rostrum, hook-shaped areas

which turn about the rostral tips of the pterygoids. In the foetal skull, they reach only slightly mesal to the pterygoids. In the adult, on the contrary, they attain almost the midline and touch the vomer. Their lateral region lies between the pterygoid mesad, which rests upon it, and the maxilla and lachrymal laterad, which it in turn overlies, the three being arranged like shingles. The caudal extremity is a thick, concave margin which surrounds the rostral end of the sphenomaxillary fossa.

Caudad to the rostrum, it is convenient to recognize mesal and lateral areas. In the mesal are the pterygoid shelf, the posterior nares, and the base of the skull. In the lateral areas are the orbits, pterygoid fossæ, temporal arches, glenoid fossæ, otic and paraoccipital regions.

In the midline the pterygoids form an elevated ledge which has a surface continuous with that of the rostrum anteriorly, but terminates in a sharp margin posteriorly where it forms the ventral circumference of the nares. This surface rostrad presents a reentrant angle in the midline. Caudad, it becomes level transversely and extends laterad on the ventrad aspect of each hamular process. The posterior naris is a single opening bordered ventrad by the pterygoids, dorsad by the smoothly concave terminal sheet of the vomer, and on each side by the deeply notched pterygoid. Caudad to the posterior nares is a deeply concave area, limited on each side by the basioccipital processes of the basioccipital which represents the base of the cranium formed by the basioccipital and basisphenoid. In the foetal skull, the exoccipital and basioccipital are not yet united, whereas in the adult the component parts of the occipital region have completely synostosed.

The orbit, as far as the bony structures are concerned, has merely a roof, unless, indeed, the slender shaft of the jugal can be considered as representing the floor. The roof most anteriorly, is formed by a narrow rim of the jugal, that portion of the ventral surface caudad to the origin of the zygomatic process. Succeeding this is the triangular, slightly concave surface of the lachrymal, placed with its tip mesad, its base laterad. The surface of this bone is marked by a groove which terminates in a blind canal leading toward the nasal cavity, though not reaching it. It is much less distinguishable in the adult skull than in the foetal. The frontal completes the orbital roof with a broad concave surface which dips under the ala orbitalis mesad, forms the entire rim of the orbit laterad, and is continuous with the ventral surface of the anti- and postorbital processes. This surface is demarcated by an elevated margin from the temporal fossa. As stated above, the bony walls and floor of the orbit have here disappeared. Of the structures forming them in the ordinary mammalian skull, the maxillary tuberosity and orbital plate of the ethmoid are entirely lacking. The lachrymal, which appears prominently in the inner wall of the orbit in many

mammals, has shifted to the roof, as has the jugal, which ordinarily assists in forming the lower portion of the rim. Moreover, owing to the loss of the inner wall of the orbit, the lachrymal and the pterygoid, ordinarily widely separated, are here in contact.

The cause of these variations from the conditions found in mammals is the suppression of the ethmoidal region of the nasal passages. This is easily to be understood when it is recalled that the maxilla owes its large expansion in the floor of the orbit to the invasion of its substance by an ethmoidal cell, and that the orbital plate is the ectal wall of the ethmoidal labyrinth.

At the junction of the orbital roof and the lateral surface of the pterygoid is an oblong recess the circumference of which is formed by the lachrymal and frontal dorsad, the palate rostrad, the frontal caudad and the pterygoid ventrad. In the mesal wall of this recess appears most caudally the tip of the ala orbitalis, perforated by the optic foramen. Ventrad to the tip of the ala orbitalis is a space bounded below by the pterygoid. This slit-like space gives passage to the nerves of the orbit and to the maxillary nerve.

Rostrad to the tip of the ala orbitalis, the area under description has for its mesal wall pterygoid and palate. This portion corresponds to the sphenomaxillary fossa of the human skull. From it leads rostrad a large canal for the maxillary nerve and artery, mesad a double canal to the nasal cavity, the sphenopalatine, and laterad a large canal which opens in the facial fossa. In the adult skull, owing to a dorsal extension of the border of the pterygoid, the region of the ala orbitalis appears shut off from the sphenomaxillary fossa. Mesal to the upward extension still lies a passage for the maxillary nerve. In the foetal skull the tip of the ala orbitalis is seen in the inner wall of the fossa only. On the other hand, in the adult it has undergone lateral growth and appears in the roof of the orbit dorsal to the pterygoid.

The pterygoid fossa occupies the entire lateral surface of the pterygoid bone. It is triangular, deepest ventrad and bifurcated caudally, owing to the notch in the caudal border of the bone. In the adult skull the dorso-caudal angle is considerably extended by the further growth of the bone in this direction, almost concealing the ala temporalis which in the younger skull is largely exposed.

The temporal arch is formed by the zygomatic process of the squamosal and the postorbital process of the frontal. The remainder of the lower boundary of the temporal fossa is made up of frontal and squamosal, respectively craniad and caudad, and the parietal and lateral border of the ala temporalis mesad. Ventrad to the temporal arch, as described above, the slender shaft of the jugal, reaching almost to the preglenoid process of

the squamosal, forms a second arch laterad to the temporal muscle; the zygomatic.

The glenoid fossa is described in connection with the os squamosum. It is essentially the same in foetal and in adult skulls, except for the greater massiveness of the bone in the latter.

The otic region comprises an area bounded mesad by the caudal end of the pterygoid and the basioccipital process of the basioccipital, laterad by the mesal border of the glenoid fossa and the paraoccipital process of the exoccipital, and craniad by the caudal border of the ala temporalis. It undergoes such considerable changes in growth as to merit close examination. In the foetal skull, between glenoid and pterygoid fossæ, a quadrilateral area of the ala temporalis is exposed. In the adult skull this is almost completely covered in by extension toward one another of the shelving edges of pterygoid and squamosum. Beneath the thin edge of the pterygoid are three openings which in the younger skull are entirely exposed. The one of these nearest the midline is that for the internal carotid artery. In the adult, merely its entrance beneath pterygoid is visible, this bone covering the opening into basisphenoid. Mesad to this opening, the pterygoid overlaps the basioccipital process of the basioccipital to a considerable degree. Laterad to the carotid opening, the pterygoid stretches caudad and actually establishes contact with the squamosum. Beneath this margin, small canals pass craniad, ventral to the root of the ala temporalis. One of these serves for the passage of the great superficial petrosal nerve. Succeeding to the point of contact of pterygoid and squamosum, just mentioned, there is a marked recession of the pterygoid border giving access to the foramen ovale. Laterad to this, the pterygoid and squamosum are again almost in contact, only a narrow strip of the ala temporalis intervening.

Examination of the younger skull shows, caudad to the ala temporalis, a large opening into the interior of the skull. The anterior portion of this opening is a deep notch in the caudal border of the alisphenoid, constituting the foramen ovale.

The posterior portion is a common opening for the cranial nerves from the seventh to the eleventh, and the jugular foramen. The larger part is occupied by the periotic, which in the young skull thus has access to the ental aspect of the skull. Its bed is formed laterad by squamosal and exoccipital, mesad by basioccipital.

In the adult skull the opening described, except for canals for the nerves, has been filled in. This had been brought about by the caudad growth of both commissura ali cochlearis and ala temporalis. The two meet and thus separate the foramen ovale from the common opening. A process

from the exoccipital extends mesad to reach the commissura ali cochlearis and divides off the canal for the seventh and the eighth nerves from that for the ninth, tenth, and eleventh caudad to it. The result of this development of bone is that the periotic is entirely shut out from the skull cavity. Into the roof of its bed enter processes from commissura ali cochlearis, ala temporalis and exoccipital. As it lies in position, it is partially overlapped laterally by a shelf of the squamosal, the processes falciformis, and held in position by a slender, crescentic process of that bone which springs from the rostral tip of that process.

The paracondyloid process in the younger skull reaches the same ventral level as the basal process of the basioccipital, from which it is separated by a deep notch at the bottom of which is the hypoglossal foramen. The exoccipital process of the squamosal fits smoothly against its cranial border. In the adult skull, this process is greatly thickened and stands out in such a manner as to lead to the formation of a notch between it and the paracondyloid process. Into this notch fits a rather massive piece of bone, the tympanomastoid, which fills it and rounds out the contour of the paracondyloid region. The tympanomastoid is also present in the young skull but only slightly developed.

NORMA LATERALIS

This view reveals especially well the manner in which the rostrum is braced against vertical strains. This is accomplished by buttresses both above and below the longitudinal axis. The first is chiefly made up of the massive premaxillæ which reach to the transverse cranial crest. The second, lighter than the first, is composed of the pterygoids which fill the gap between the base of the rostrum and the basioccipital processes of the basioccipital.

The lateral aspect of the rostrum is formed, to a great extent, by the maxilla, though the distal section shows only the premaxilla, which rises above the former nearly its whole length disappearing as the caudal extremity is approached. The margin of these two bones show a continuous alveolar gutter, much more distant in the smaller skull, as it is filled with porous bone in the adult. The articulation of palate and maxilla, and pterygoid and palate, are well seen at the rostral base. There are no essential differences between the two skulls in respect to these structures. An excellent view of the pterygoid is gained from this direction.

The prominence of the maxillary tuberosities in the older skull should be especially noted. It is the enlargement of these which forms the most distinguishing mark of the *Hyperoodon* skull and *Ziphius* is the nearest to

Hyperoodon in this respect of the ziphioids. The greatly increased depth of the facial fossa brought about by age will at once be noted.

The frontal is tripartite on this aspect, showing preorbital and postorbital and ascending processes. Behind the ascending branch of the frontal, the deep temporal fossa and, in its depth, the squamoparietal suture are seen. This suture is much more irregular in the grown skull. The squamosum shows three divisions: squamous, glenoid, and exoccipital. The latter is, in the young skull, a thin hook-like process; on the other hand, much more massive in the old, wherein it assists in forming a notch for the reception of the tympanomastoid. Between the glenoid and exoccipital processes is a well-marked notch for the passage of the external auditory meatus.

NORMA OCCIPITALIS

On occipital view the skull takes the form of a massive arch which supports itself on the tympanomastoid and paraoccipital processes. The inner contour of the arch is formed by the basioccipital processes of the basioccipital, united across the midline by the body of that bone. In the space outlined by these structures is seen the posterior nares, walled rostrad by the pterygoids. Laterad to the nares are the pterygoid notches. In the center of the arch, close to the ventral margin, is the foramen magnum. This opening is circular except for the presence of two projecting nodules of bone along the dorsal border.

On either side of the foramen magnum are the condyles. These are semielliptical masses of bone placed with their long axes passing lateromesad and ventrad. Their lateral margins are markedly convex; their mesal margins, slightly concave. In the foetal skull, a raised area on the basioccipital, only slightly demarcated from those portions of the condyles born on the exoccipitals, joins them into a single horseshoe-shaped articular surface. This is of interest as the same condition is found in the chondrocrania of certain other mammals (*Talpa*; E. Fischer). All trace of the central area has disappeared in the adult.

Dorsad to the foramen magnum, a vertical crest leads nearly to the summit of the skull. This is joined on either side, near its termination, by crescentic lines which lead to the margin of the temporal fossa. These lines bound slightly depressed areas for the attachment of muscles.

The circumference of the arch marks the outline dorsally of the great transverse crest of the cranium. Midway along the outer border, a great gap in the contour appears, which marks the site of the temporal fossa. This is bridged over by the frontal bone and its postorbital process. Ventrad

to the temporal fossa, massive projections on either side are formed by the squamosals and their zygomatic processes. From their apices, the bone falls away to the level of the paracondyloid processes. Three bones are involved in the formation of the pedestals of the arch described. Rostrad is the exoccipital process of the squamosal. Caudad appears the massive paraoccipital process of the exoccipital. The deep notch which lies between the extremities of these two is filled in by the tympanomastoid. This process, small and flattened in the young skull, becomes massive and rough in the adult.

INTERIOR OF THE SKULL

Cranial Floor.—The floor of the cranial cavity is distinguished by its great proportional breadth. To bring this about, structures ordinarily found in the side wall of the mammalian skull, as in man, have been turned down into a horizontal position. There is, in addition, an actual caudo-rostral shortening, owing to the almost complete suppression of the anterior cranial fossa. Those parts which in the human skull form the floor of this fossa, the mesethmoid, cribriform plate, and the orbital plates of the frontals, are in the skull of *Ziphius* transferred to the rostral wall. Of the structures ordinarily found there, only the alæ orbitales remain in the floor.

The main mass of the cranial base is made up of the fused basioccipital and basisphenoid, which occupy the midline. The basioccipital is wedged-shaped caudally, its apex reaching the foramen magnum. On either side of it are narrow ledges of the exoccipitals, which here have a horizontal position. Immediately rostrad, it occupies the full width of the cranial floor, its body being extended to each side by the basal processes. It should be noted that the basioccipital occupies fully half of the caudo-rostral extension.

In the sphenoidal region, the width established caudally is fully maintained by the basisphenoid, to which are fused, on each side, the processes alares and their caudal prolongations, the processes alæ cochleares. Laterad to these still is a large gap which represents the confluent posterior and middle lacerated foramina.

Rostrad to a line drawn through the carotid foramina, the transverse measurement receives an increase by the addition of the alisphenoids. These structures spread out laterad and all the region mesad to the groove for the middle meningeal artery lies in the base of the skull. Laterad to the groove mentioned, they are overlain by a sheet of the parietal.

The presphenoid and the alæ orbitales, the latter separated from the alisphenoids by the sphenoidal fissure, complete the cranial base rostrad.

Contrary to the condition found in most mammals, the basioccipital slopes dorsoventrad for a considerable distance rostrad to the foramen magnum. This is owing to the fact that a great part of the bone here develops in an epichordal position. The sloping area is succeeded by a horizontal portion to which follows the short upward rise of the presphenoid. Thus the cranial floor is concave caudorostrad. Transversely, it is horizontal throughout.

In the occipital region, on either side, can be seen the ental openings of the hypoglossal foramina. Further craniad, in the midline, is the orifice of a small canal which passes completely through the bone, bifurcating ectad so as to present two opening places, one to each side of the midline. A considerable portion of the occipital region and the whole basisphenoidal region are bordered by the confluent lacerated foramina. These can be seen to be divided into three by two paired protrusions from the lateral and mesal borders. They transmit, in addition to large vessels, the vagus group of cranial nerves, the seventh and eighth, and the inferior maxillary branch of the fifth nerve. The secondary opening for the seventh and eighth nerves is peculiar, among mammals, to cetacea. The closure of lacerated foramina in the adult has already been described in connection with the norma basalis.

The dorsum sellæ is a scarcely distinguishable ridge. The sella turcica is a very shallow fossa. In its concavity is the ental orifice of the hypophysial canal which still completely perforates the bone. In the same transverse plane as this, laterad to it, are the carotid foramina with grooves leading from them rostromesad. The intersphenoidal suture is still rather widely open. It is separated from the sphenoidal fissure on each side by only a small bar of bone.

The groove for the optic chiasm is narrow, but of unusual lateral extension, owing to the great width of the alæ hypochiasmaticæ.

Caudal Wall of the Cranial Cavity.— The caudal wall of the cranial cavity is formed by the exoccipitals in conjunction with the supraoccipital. There are three openings in this wall. In the midline, ventrally, is the hexagonal foramen magnum. In the circumference of this lie (above) the exoccipital, (below) the basioccipital, and (to either side) the exoccipitals. Dorsolateral to the foramen magnum are the paired lateral occipital fontanelles. These are bounded by the exoccipital, supraoccipital, and, rostrad, by the parietal bones. The foramen magnum is framed by an arched ridge, described in connection with the separate bones, which gives attachment to the tentorium. From its summit extends a great median crest which is formed through ossification of the falx cerebri. The ridges and the crest should be particularly noted, as they have much to do with reinforcing the skull against anteroposterior pressure. They bound broad shallow fossæ which lodge cerebellum and the occipital lobes of the cerebrum.

Anterior Wall of the Cranial Cavity.—The rostral wall of the skull is, in the main, composed of the great vertical sheet of the frontal bones. Each presents a uniformly concave, semicircular surface with a curved dorso-lateral and sinuous ventromesal margin, which rises lateromesad. The two surfaces meet mesally to form a narrow isthmus and the frontal fontanelle ventrad. These two bones are like a pair of saddle bags joined by their strap. The great notch which lies between them is partially filled in by the mesethmoid and structures closely related thereto, and may be said to be homologous to the ethmoidal notch of the human skull. It will be noted, however, that this opening extends far beyond what may be considered the limits of the ethmoidal notch, and is better designated as the frontal fontanelle.

In the adult skull, as may be ascertained by inspection through the foramen magnum, the frontal fontanelle and the ethmoidal notch are completely filled in by a smooth surfaced sheet of bone. Two small openings are present, canals which open by three mouths in the nasal passages. These are for the nasal branches of the fifth nerve.

Laterally the frontals extend to the ventral limit of the wall a rather broad process which articulates with the tip of the alisphenoid. Mesal to this, the border of each presents a deep notch which receives the tip of the ala orbitalis. Proceeding mesad are seen small areas of the pterygoids; then the extremities of the sphenoidal turbinates overlapped by a second salient of the frontal margins. The mid-space is occupied by the mesethmoid, which rises vertically and is flanked by the ectethmoids.

Between the sphenoidal turbinate and the ala orbitalis is a fissure which represents the posterior ethmoidal foramen of the human skull. On each side of the mesethmoid is a small fissure which may allow passage for the nasal nerves from the cranial cavity to the nasal passages.

Ventrad to the mesethmoid and ectethmoids, a narrow strip of pre-sphenoid is turned dorsad and forms the ventral limit of the wall in this region.

The notable thing in connection with this wall of the skull is the presence in it of pterygoids, sphenoidal turbinates, mesethmoid, and ectethmoids. These are all structures which in other mammalian skulls appear in the floor of the anterior fossa. The impulse for their shift from the floor to the rostral wall undoubtedly comes from the suppression of the ethmoidal region of the nasal cavities and the turning dorsad of their external orifices.

Lateral Wall of the Cranial Cavity.—The lateral wall of the cranial cavity is formed, in the main, by one bone, the considerably compressed parietal. This is a most striking indication of the great caudorostrad compression of the skull. Caudally, a small portion of the exoccipital appears. Rostrally,

the side wall ends at the parietofrontal suture. The tip of the lateral occipital fontanelle appears above the exoccipital in the notch between it and the parietal. Dorsal to the parietal, the supraoccipital completes the side wall. On the ectal aspect of the parietal lies the squamosal, completely shut out of the cranial cavity. It aids in reinforcing this wall against pressure. Another structure ordinarily found in the side wall of the mammalian skull, the alisphenoid, has been, as I have mentioned, transferred to the floor, so that two structures added to the reptilian brain-case to form that of the mammal are secondarily shifted in this highly developed mammal, one entirely out of the brain-case, the other to the floor.

The impulse to the broadening of the brain-case is probably to be found in the suppression of the ethmoidal region. This leads to the disappearance of the anterior cranial fossa and a consequent compression of the brain caudorostrad, which forces it to seek lateral expansion.

NASAL PASSAGES

The nasal passages take a crescentic course from the anterior to the posterior nares, the convexity of the curve being rostrad. The external orifice is much deflected to the left; whereas the internal is perfectly symmetrical.

The anterior nares in the younger skull form a single orifice, owing to the incompleteness of the mesethmoidal ossification and the absence of the cartilage. In the fully developed skull, the nares are separated almost to the level of the premaxilla by a sharp dorsal margin of the nasal septum formed by the upward growth of the vomer and ectethmoids. In both young and old, the lateral boundaries of nasal openings are formed by the premaxilla and, in both, the nasal bones overhang them caudally. The septum in either skull is made up of the mesethmoid with an encasement of vomer and ectethmoid. In the young skull, this encasement is only partial; in the fully developed skull, on the other hand, the encasement is complete, as already described.

The outer wall of each nasal passage is formed ectoentad by premaxilla, a broad surface of maxilla, a narrow strip of palate and then by a section of pterygoid as broad as the others taken together. These elements are distinct in the young skull but completely amalgamated in the older and their boundaries can not be distinguished.

The rostral wall is established by the turn mesad of the maxillæ, palates, and the pterygoids to meet the septum. Ventrad to the level of the septum, in the common nasopharyngeal passage, the rostral wall is made up entirely by the pterygoids meeting in the midline.

The caudal wall differs considerably in the two skulls. In both, the nasals appear overhanging the external orifices. In the young skull, ventrad to the nasals, is a large gap which allows free communication between the nasal cavities and the interior of the cranium. This is homologous, in part at least, to the ethmoidal notch of the human frontal bone. Laterad to the notch, a roughened margin of the frontal bone appears in the wall. Ventrad to the notch, the ectethmoidal plates and the sphenoidal turbinates are present, and, finally, the horizontal sheet of the vomer. In the adult skull, except for certain openings to be mentioned later, the whole caudal wall of each nasal passage appears as a smooth sheet of bone. This is doubtless brought about by the fusing of vomer, sphenoidal turbinate, and ectethmoid and by their dorsal extension concomitant with the upward growth of the septum. It is probable that the frontal also helps to fill in the gap of the frontal fontanelle, so that finally the nasal cavity is separated from brain cavity by a double layer of bone, the frontal composing one layer, and the fused vomer, sphenoidal turbinal, and ectethmoid the second.

The terminal portion of the narial passages is undivided and approaches the horizontal in direction. The roof is formed by the horizontal portion of the vomer and a small strip of each pterygoid. Outer wall and floor are formed by the pterygoids.

Through the outer wall of each nasal passage, two small canals lead to the sphenomaxillary fossa. These are the sphenopalatine openings and they are found alike in both skulls. One is entirely enclosed in the palate bone; the other lies between palate and lachrymal ectally, and palate and tip of sphenoidal turbinate entally.

It has been mentioned that the large frontal fontanelle communicating with the brain cavity in the young skull is closed in the adult. At the site of this orifice, three small canals may be seen in the adult skull. They have a common opening entally and transmit the nasal branches of the ophthalmic. In this same region is a structure not present in the foetal skull, a crescent of bone secured by its tips to the dorsal wall and so forming a projecting loop. This may be a vestigial turbinate.

Three classes of forces may be thought of as acting upon the skull of cetaceans: water pressure; the vertical and lateral twists and strains upon the prolonged rostrum; and those incident to propulsion, due to the resistance of the water in front and the thrust of the vertebral column upon the condyles behind.

Response to water pressure takes the form of a general thickening of the cranial walls. This is most manifest where the bones are most directly exposed to the pressure along the transverse crest, and at the extremities of that structure. On the other hand, in the basal region, where the overlying

soft parts are thick, the bone has a tendency to be thinner. In the occipital region, however, the ridges which mark the ental surfaces of the bones undoubtedly are reinforcements against compression.

For convenience, the skull of *Ziphius* has been described as consisting of the rostrum and the cranium proper, the line of division being drawn tangent to the rostral borders of the maxillary tuberosities. It is well to note, however, that structurally such a division is arbitrary. The rostrum expands at its base in both the vertical and the transverse diameters. The transverse expansion, effected by the broadening of the maxillæ, reaches its extreme in the region of the maxillary tuberosities, so that their rostral borders, indeed, furnish a valid line of demarcation between rostrum and cranium in the transverse plane. On the other hand, the vertical expansion, formed on the dorsal aspect of the skull by the premaxillæ, on the ventral aspect by the broad pterygoids, extends much further caudad to the occipital region. Thus, in this plane, it is difficult to settle on a point where the rostrum ends and cranium begins.

The former is, in reality, merely the apical portion of a pyramidal mass which rests its base against a ring formed by the supraoccipitalis, parietals, and the basisphenoid. The junction of the occipital ring and the base of the rostrum results in the formation of the great transverse crest of the cranium. From the crest, both caudad and rostrad, the bone falls away toward the foramen magnum on the one hand and rostrum on the other, so establishing the caudal and rostral walls of the cranial cavity. It is the wide expansion of the rostrum at its base which results, in spite of the great length of the structure, in the firmest security against all manner of strains.

In the vertical plane, forces are transmitted from the rostrum to the occipital ring chiefly through the frontal portions of the premaxillæ. The chief strength is not gained through direct contact, for only the right premaxilla reaches the crest of the frontal and that by a narrow process. Between the premaxillæ and the frontals are interpolated the massive nasal bones, and it is by them that thrusts are in the main supported. The surfaces of contact between nasals and premaxillæ are broad and the articulations very firm.

In union with the premaxillæ, the maxillæ also turn dorsad and reach the transverse crest. This portion of the maxilla, however, is merely a thin sheet of bone and can contribute no great strength in this direction.

On the ventral aspect of the skull, the lines of the transmission of force lie through the pterygoids. These bones have a broad articulation with the base of the rostrum, chiefly with the palates which are interposed between them and the maxillæ. They form, also, a small direct articulation with the maxillæ and have a very slight contact with the vomer. The union,

then, is one of great strength. Caudally, the pterygoids reach the bases of the basioccipital processes in the occipital region.

The ventral brace thus formed is much less firm than the dorsal, since the pterygoids are less massive than the premaxillæ and the structure of the bone is less dense. Moreover, dorsal strains are transmitted through a continuous line of bone, whereas the ventral strains must pass through three articulations. We may conclude then that strains in this direction are not so severe as those in the opposite. However, in the adult skull, provision for greater firmness is made by the growth laterad of the borders of the pterygoids, which thus secure a very firm hold on the base of the skull.

Lateral strains are provided against by the expansion of the base of the rostrum in the transverse plane. This is effected, as already stated, by the spreading out of the maxillæ. Through them, forces reach the occipital ring along two lines. One is an inner, along the lateral cranial wall, formed chiefly by the parietals, which articulate directly with the exoccipitals. There is, in addition, an outer line of transmission through the postorbital processes of the frontals to the jugal processes of the squamosals and hence to the exoccipitals. That the lines of greatest strain lie through the lateral margins of the bones is at once evident from their formation. Mesally, both the maxillæ and the frontals are thin sheets which lie in contact and form a firm articulation preventing displacements, indeed, but offering no great resistance to compression. Their lateral margins, on the other hand, are thicker. The frontals form the massive orbital processes. These thrust forward strong preorbital processes which are locked to the maxillæ by the lachrymals. Lighter postorbital processes reach the jugal processes of the squamosals, which interlock with the exoccipitals.

Additional security is given to the rostrum by the character of the articulations of the bones forming it with those of the cranium. On the dorsal aspect, the chief of these is that between maxilla and frontal. Both of these bones expand into broad sheets, deeply concave rostrally, the maxilla fitting into the concavity of the frontal. The premaxillæ fit over the mesal margins of the maxillæ and secure this border to the nasal and frontal.

On the ventral aspect, the pterygoid has a broad contact with the base of the rostrum and spreads over the base of the cranium to the basioccipital.

Two characteristics, then, distinguish these articulations: their breadth and a certain amount of interlocking.

The response to the forces incident to propulsion manifests itself in the formation of the great transverse crest of the skull. The condyles lie above the plane of the cranial base. Consequently forces acting through them would tend to compress the vertex of the skull, provided there were at the same time firm resistance from in front, such as the water provides when the

animal is swimming; hence the compression of the dorsal areas of the frontal and parietal bones and the piling up of the supraoccipital on the one hand, and the premaxillæ, the maxillæ, and frontals on the other, into the transverse crest.

This structure is the central architectural feature of the ziphioid skull. It consists of massive lateral piers connected by a more slender arch. The manner in which the rostrum braces itself against the lateral piers and crest of the arch has already been described. The resistance of the water is undoubtedly transmitted to the transverse crest along the same lines as the forces which tend to twist and bend the rostrum.

It remains to examine the manner in which the thrusts upon the condyles are transmitted to the transverse crest. Upon the ental surface of the occipital region, three ridges are seen to meet at a point just dorsal to the foramen magnum. The dorsal of these is single and extends to the apex of the transverse crest. The ventral are paired and symmetrical. Their distal extremities terminate in the lateral masses already described, so that the portions of the transverse crest supporting the greatest strains from the rostrum are the very ones to be most strongly reinforced from behind.

Forces are likewise transmitted from the condyles through the basioccipital processes along the line of the pterygoids to the rostrum. These ventral lines of transmission are slighter than the dorsal and are of less importance, as would be expected from the dorsal position of the condyles.

BONES OF THE ROSTRUM

The bones entering into the formation of the rostrum are the maxillæ, the premaxillæ, the vomer, pterygoids, and the palates. The main mass is composed of the three first mentioned, the two latter pair lying in the base on the ventral aspect.

The Maxillæ.—The maxillæ, owing to the marked sinistral deviation of the nasal passages at their external orifices, are asymmetrical. In the rostral region, the right bone is broader and more massive; in the frontal, it is of greater breadth and more marked curvature, with more extensive articular surfaces. The rostral portion has three surfaces. The dorsal of these has been sufficiently described in connection with the dorsum of the rostrum. The lateral surface appears largely on the venter of the rostrum. A portion near the base, it will be remembered, is covered by the palate and pterygoid. Between the articular area and the border of the bone, a small furrow leads over the lateral border, affording passage to the facial vessels and nerve. The articular surface is grooved by the posterior palatine canal.

The mesal surface presents a series of depressions separated by ridges. The most dorsal of the ridges is a round margin, more prominent in the left bone, which lies along the line of the articulation with the premaxilla. Distally, on the left side, it is interrupted by a groove which leads into the premaxillary canal. On the right side, the border itself is complete, the groove being replaced by a canal which burrows under it.

Immediately ventrad to the marginal ridge is the articular surface for the premaxilla, which extends the whole length of the bone. The caudal two-thirds is concave. The rostral one-third is divided by a longitudinal crest, which marks the surface relief of the alveolar gutter. This crest fits into a depression of the premaxilla. Dorsal and ventral to it are longitudinal concavities which receive corresponding elevations of the opposing bone, the two thus firmly interlocking.

The premaxillary surface is limited below by a high, sharp ridge which juts out at a right angle. This is designated as the vomerine shelf. It leaves the center of the border of the bone at an acute angle and is continued caudad as the mesal margin of the frontal portion. Its shelf-like character is more marked on the right bone. Ventral to this ledge, the articular area for the vomer occupies a triangular space with its apex at the center of the ventral border, its base at the caudal limit of the rostrum. It is deeply concave, owing to limiting crests dorsad and ventrad. The surface aspect is longitudinally striated and grooved by furrows which form canals in the articulated state.

The inferior border of the maxilla at its apex is smooth and rounded. Passing caudad, it becomes an exceedingly sharp margin which so closely embraces the vomer as to make the suture difficult to ascertain. Caudally, this crest is continued on to the ventral surface of the frontal portion, gradually becoming lower.

As it joins the cranium, the maxilla lies at first vertical with its surfaces facing mesad and laterad. Passing caudad, the bone rotates on a longitudinal axis and undergoes that great transverse broadening to which the expansion of the rostral base is due. The horizontal sheet then curls upward till it becomes vertical and enters into the rostral face of the skull. The border which embraces the external circumference of the frontal sheet begins rostrally at the maxillary tuberosity. From this point, a rough margin encloses nearly the half of a circle and meets the internal border at the dorsal limit of the premaxillary articulation. The internal margin which joins the ends of the half circle is a continuation of the vomerine shelf. Near its dorsal termination, it becomes lower and is replaced by a high ridge which rolls laterad, designated as the facial crest. Over the convexity of this crest fits the premaxilla to form an interlocking articula-

tion. The surface thus delimited appears on the dorsorostral wall of the cranium and is sufficiently described in connection with that region.

The caudoventral surface of the frontal sheet has the same borders as those described for the rostrrodorsal. It presents also a like change in its plane, the most rostral portion facing laterad, the caudal portion caudoventrad.

The vertical portion of the surface is largely taken up by the articular surface for the palate. It is grooved centrally for the posterior palatine canal. Its lower margin is continued on to the caudoventral surface of the body as a ridge which unites with the margin of the vomerine crest. Mesal to this ridge, the ventral surface of the vomerine crest presents itself with a rough area rostrally for articulation with the mesorostral cartilage. Caudal to this, clearly demarcated from it, is a broad, smooth surface which forms part of the rostral wall of the nasal fossa.

Lateral to the dividing ridge, three bones articulate with the crescent-shaped surface. Rostrally at the tip of the crescent is a small triangular area for the jugal. Caudal to this is a lozenge-shaped area for the lachrymal. These two are scarcely delimited one from the other. They are overlapped mesally by a sharp ledge passing from the maxillary prominence to the lateral aspect of the infraorbital canal. The surface for the lachrymal is grooved for a canal, completed by the articulation which leads from the rostrrodorsal surface to the infraorbital foramen.

The remainder of this surface articulates with the frontal. It is, in the main, smooth but presents shallow grooves for vessels which are completed canals in the articulated state.

The Premaxillæ.—The premaxillæ present to an even greater degree the asymmetry of the maxillæ. The rostral processes are much the same on the two sides. Of the bodies, however, the right is broader and shows more extensive surfaces of articulation. Indeed, it may be said that it is in the flaring of the mesal border of the right premaxilla that the deviation of the nares to the left is most clearly expressed.

The lateral surface of the rostral process is divided by a high ridge into articular and non-articular areas. This ridge is the external relief of a canal passing the full length of the interior of the bone. Ventral thereto, there is a deep longitudinal depression bounded below in its turn by a marginal crest. The depression receives an elevation of the maxilla about which the ridges lock. Dorsal to the articular surface is a smooth elongated area which appears on the dorsal surface of the rostrum.

The mesal surface of the rostral process of the premaxilla presents a smooth concave surface with elevated margins. Of these, the upper is free. The lower, for the caudal three-fourths of its extent, articulates with the

vomer. For the proximal one-fourth, it articulates with its fellow on the opposite side. By these articulations is formed a smooth-walled, broad furrow on the dorsal aspect of the rostrum, the mesorostral gutter which has been described in connection with the dorsum of the rostrum.

The upper border of the vomerine gutter is a sharp, free edge which delimits it from dorsal aspect of the rostrum. Caudally, this margin divides to form the borders of the dorsal surface of the frontal portion of the bone.

The ventral border of the premaxillary rostral area is, in reality, a broad surface, being the ventral aspect of the marginal crest of the lateral surface. Rostrally, this surface is free and appears on the ventral face of the rostrum. Caudally, the whole surface, narrow here, articulates with the dorsum of the vomerine shelf of the maxilla and with the margin of the vomer.

Frontal Portion of the Premaxilla.—The distal limit of the dorsal surface of the frontal portion of the premaxilla may be placed at the premaxillary foramen. The dorsal border splits just rostrad of it and embraces a narrow concave surface, in the depth of which is the canal. The remainder of the surface on the right side is broad, smooth, and concave rostrocaudally. The mesal margin deviates widely to the left and, at its middle, is produced into a tubercle which is in close relation, in the foetal skull, with the mesethmoid ridge. In the adult, it forms a short articulation with the mesethmoid and, for the rest of its extent, presents a gently concave margin overhanging the nasal fossa.

The lateral margin is sinuous, convex rostrally and caudally with a concave area between. It is sharp for its rostral one-fourth and overhangs the maxillary articulations. Its caudal three-fourths broadens into a narrow surface which limits mesally the great frontal fossa of the maxilla.

The dorsal surface of the left premaxilla is much narrower than that of the right. It is delimited by elevated margins which render the surface concave transversely as well as rostrocaudally. The borders meet again as they approach the dorsal tip, the surface being thus replaced in the dorsal one-fourth of the process by a sharp crest. The mesal border, in contrast to that of the right bone, deviates laterad, sharing the displacement of the nasal fossa, and is concave in its general formation — the tubercle, so prominent on the mesal border of the right bone, being only slightly indicated. It has the same relations to the rostral gutter, mesethmoid, and nasal fossa as the corresponding border of the right bone, though its articulation with the mesethmoid is more extensive.

The ventral surface of the frontal portion of the right premaxilla is convex in its general conformation. Rostrally, it is marked by a high axial ridge, the prolonged lower border of the rostral region which fits into the

vomerine shelf of the maxilla. Caudally, this ridge splits into two elevations which later becoming more prominent can be traced to the caudal limit of the bone. A small area near the mesal border rostrally articulates with the mesethmoid. Caudad to this is a smooth surface which enters into the wall of the nasal passage. Owing to the marked mesal projections of the margin, this nasal surface on the right side forms part of the mesal roof as well as of the outer wall. The caudal extensions of the low ridges above mentioned limit a longitudinal depression which embraces the facial crest of the maxilla. All the articular areas are rough and furrowed for vessels. The ventral surface of the body of the left premaxilla differs from that of the right bone only in being much narrower. The axial ridge fits closely into a deep furrow formed by the vomerine crest of the maxilla, security of articulation being secured in this case rather by depth of interlocking than by breadth of contact. The nasal surface does not overhang the nasal passage and so forms only an outer wall, not a roof, for that structure.

In the adult, both bones appear to have increased more in dorsoventral extent than transversely. Thus the surfaces appearing in the nasal passages and frontal fossæ are much greater proportionately than in the foetal skull. Regarded as a whole, the frontal portion of the right bone appears triangular on cross-section with surfaces appearing in nasal passage, frontal fossa, and on the dorsum of the skull. The corresponding portion of the left bone appears as a vertical sheet with surfaces facing mesad in the nasal passage and laterad in the frontal fossa. The dorsal surface, so prominent on the right side, is comparatively insignificant. The two divisions of the bone appear to have different relations to each other on the two sides. On the right side, the frontal portion lies in the same longitudinal axis as the rostral. On the left side, the axis of the frontal portion shifts laterad and so forms a blunt angle with the axis of the rostral. This deviation of axis is owing to the encroachment of nasal passages on the left.

The Vomer.—The vomer, resting its expanded base against the ventral surface of the cranium and extending its pointed apex to within two inches of the tip of the rostrum, forms the central stem of that structure. The dorsal surface, concave and of smooth aspect, makes up a considerable part of the rostral groove. The ventral surface, convex throughout its extent, presents an axial ridge. This becomes high and sharp caudally and terminates in a spur which demarcates the rostral from the narial region. Both near its tip between the maxillæ and near its caudal termination between the pterygoids, the ridge appears on the ventral surface of the rostrum. The surface on either side is entirely overlain by the neighboring bones — for the greater part by the maxillæ. Near the caudal extremity are small areas for the palates and pterygoids. The surface of each maxilla wherewith the

vomer articulates is deeply concave, terminating above in the vomerine shelf and below in a strongly salient border. Thus it is firmly locked in its place and binds the maxillæ together and them in turn to the base of the skull.

At its caudal extremity, the vomer expands in such a manner as to form a broad sheet of bone concave transversely owing to the turning downward of the lateral margins. This sheet by its dorsal surface has an extensive articulation with the base of the cranium. Its caudal edge reaches the basioccipital. Its lateral borders overlap margins of the pterygoids and secure them to the skull. The ventral surface assists largely in the formation of the nasal cavities.

On either side of the mesethmoid there extend upward from the cranial edge of the vomerine plate flat strips of bone which reach the vertical height of the alæ orbitales. They incline laterad as they pass upward and lie along the lateral margins of the ectethmoid with which they tend to fuse. Their lateral borders override, rostrad, the mesal edge of the pterygoids and are in turn overlapped by the palate. The dorsal margin passes rostrad to the ventral edge of the frontal. These processes have a concave nasal surface which in union with the pterygoid forms the caudal wall of the nasal passage. Their convex caudal surface in part lies against the sphenoid and in part faces the cranial cavity. The position of these processes suggests that they are homologous to the sphenoidal turbinates of the mammalian skull.

The Pterygoid.—The pterygoid extends from the base of the rostrum to the cranial margin of the basal process of the basioccipital affording a powerful brace to the ventral aspect of the cranium. The bone is quadrilateral in shape, having two long rostral and two short caudal borders, one of the latter interrupted by a wide indentation. The lateral surface shows an extensive shallow fossa deep in the ventral and dorsal regions — less so centrally, owing to the presence of a wide convexity. The circumferential depressions are caused chiefly by the elevation into sharp ridges of all the borders. The central convexity is the external expression of the cylindrical nasal passage of which the bone in this region forms the lateral wall.

The mesal surface is divided by ridges into two articular areas and a nasal. The ridges greatly increase the thickness of the bone and give a corresponding increase in strength. The first is really the prominent ventral border. It is high and wide at its summit and bent at an obtuse angle near its rostral extremity. The portion rostrad to the angle articulates with the ventral ridge of the vomer. The remaining portion of the ridge meets the opposite pterygoid in the articulated condition, forming a median longitudinal suture in the rostral wall of the nasopharyngeal passage. The

second longitudinal ridge lies near the dorsal border. It is high and sharp at its summit, broad at its base, and its course presents a convexity ventrally. This ridge fits into a fissure between the lateral margin of the vomer, on the one hand, and the presphenoid, on the other. Its cranial extremity tends to become vertical in direction and bears on its summit a cup-shaped cavity for articulation with the lachrymal.

The third ridge is vertical in direction and connects the cranial ends of those already described. Though low in the greater part of its course, its dorsal extremity becomes elevated and bounds mesad a recession which receives a protuberance of the palate.

The first articular area lies craniad to the third ridge. It is triangular, smooth, and flat, except dorsad where there is the recession mentioned above. The greater part of the surface articulates with the palate bone. Near the ventral border is a small area for articulation with the maxilla.

The surfaces of the dorsal longitudinal ridge form the second articular area. The ventral has a large area for the vomer and a smaller rostral area for the sphenoidal turbinal. The dorsal surface shows an oblong, centrally placed, concave area for articulation with the ventral surface of the ala hypochiasmatica, and rostral to this a smaller region which, for the most part, articulates with the ala orbitalis but along its mesal border appears in the cranial cavity. At its caudal margin, this surface articulates laterally with the ventral aspect of the ala temporalis, mesally with the basisphenoid. The two areas, that for basisphenoid and that for the ala temporalis, are separated by a groove which allows passage to the great superficial petrosal nerve. The balance of the surface lies close to the ala orbitalis without contact. In the articulated state it forms the lateral wall of a recess ventrolateral to the ala orbitalis leading from the sphenoid fissure to the sphenomaxillary fossa.

The nasal surface is smooth-walled and uniformly concave dorsoventrad. It forms the lateral wall of the nasal passage.

The dorsorostral border is thin. The rostral two-thirds lies along the articulation of the pterygoid and palate. The caudal one-third, at a slightly higher level than the rest, bridges over the space between palate and greater wing of the sphenoid, forming a free edge ventrad to the apex of the orbit.

The ventrorostral border forms a fairly wide, slightly concave surface. Rostrally, where the two pterygoids articulate, they together make up a shallow fossa of considerable width. Caudally, the two surfaces diverge.

The caudoventral border presents two processes, separated by a wide notch. The ventral process, deeply concave laterad, corresponds to the hamular process of other mammals. The dorsal process articulates by its tip with the basal process of the basisphenoid.

The caudodorsal border articulates its full length with the rostral border of the ala temporalis.

There is evidence in the appearance of the pterygoid of two ossification centers. This takes the form of a slight fissure at the center of the pterygoid notch and of shallow grooves lining both surfaces leading rostrad from this notch. These appear to divide the bone into two portions, which join with shelving margins. The one includes the hamular process and the portion articulating with the palate; the other, placed more caudally, articulates with the pre- and basisphenoids. The significance of the double ossification center is hard to determine from the evidence at hand. It may be that the rostral and hamular processes represent the true pterygoid, and the more caudal portion the external pterygoid plate of the basisphenoid. On the other hand, as it is hard to accept an external pterygoid place which ossifies separately from the basisphenoid, it seems best to consider the whole structure as a pterygoid which ossifies from two centers and to find the external pterygoid plate fused to the body of the sphenoid as described in connection with that bone.

Rostrum.— Having considered the various elements of the rostrum separately we may now bring out the general principles on which it is built and attached to the cranium.

1. The articulation of the bones among themselves are interlocking. This is shown by the manner in which the alternating ridges and depressions of the maxillæ and premaxillæ fit into one another.
2. Approaching the cranium, the articulations become broad as well as interlocking.
3. The extensive mesorostral ossification in adult and especially in male skulls gives great additional strength to the rostrum.
4. The rostrum is braced against lateral and vertical strains by the great expansion of its base.
5. The vomer assists in uniting the bones of the two sides across the mid-line, furnishes a center of ossification for the mesethmoid cartilage, and unites the whole rostrum directly to the base of the skull.

The Lachrymal.— The lachrymal is a rather massive bone of sufficient breadth and length to form a considerable part of the roof of the orbit. The broader division lies laterad and thrusts its thickened rough margin to the edge of the rostral base, appearing as a border prominence just behind the antorbital notch. The apex reaches the inner recesses of the orbit, where it lies in a cup-like process of the pterygoid close to but not actually in the nasal cavity.

The main mass of the bone is in the shape of a disk. The dorsal surface of this is convex mesad, slightly concave laterad, owing to the elevation of the lateral margin. This concavoconvex surface opposes a depressed

region on the ventral surface of the maxilla which possesses reciprocal elevations and depressions. Along its rostral margin is a crescentic area for articulation with the jugal, which thrusts itself between lachrymal and maxilla.

The ventral surface of this section is, in the main, deeply and uniformly concave. This is the more marked in that the lateral margin is considerably decurved. Along the mesal edge is a smaller area delimited from the general surface by a caudorostral ridge. The rostral portion of this area is overlapped by a ledge, on the ventral surface of the maxilla, which assists in locking the bone firmly in place. A small caudal triangular portion appears in the roof of the orifice of the infraorbital canal. The caudal border of this, again, is overridden by a slight projecting ledge of the palate.

The lateral portion of the circumference of this section is taken up by a narrow groove, which receives the margin of the frontal. The lower edge of this groove is especially prominent and firmly supports the frontal from beneath. The grooved area is succeeded by the rough region already described as appearing beneath the lateral border of the maxilla. The rostral border is contained in the cup-like body of the jugal. The mesal margin lies under a ledge of the maxilla and terminates in a triangular projection which reaches the palate. The caudal border gives rise to the hook-like projection now to be described.

The caudal portion of the lachrymal is separated from the body of the bone by a deep indentation of the mesal margin which effects the formation of a neck. The bone becomes narrow in its transverse measurement, broader vertically, reversing the conditions found in the body. The whole process turns mesad and it terminates in a sharp vertical crest.

The laterocaudal surface is continuous with the grooved lateral margin of the body. It articulates, in part, with the base of the mesal edge of the orbital process of the frontal. Ventrad to this, there is a narrow strip which appears in the circumference of the apex of the orbit.

The mesoventral surface presents, first, a deeply concave area which partially surrounds the mesal opening of the lateral maxillary canal. A small spur on this surface marks off a secondary channel from the main one. Ental to the depressed area is one more elevated. By this surface, the lachrymal articulates in succession dorsoventrad with the maxilla, the palate by slightly interlocking surfaces, and with the pterygoid in a cup-like depression in which it rests its rounded extremity. Between the last two articulations is a furrow which bridges over a channel in the palate.

The dorsal surface is concave and lies against the maxilla, enclosing with it a vascular canal. The ventral surface appears, for the most part, free in the roof of the inner region of the orbit. The tip of this surface joins

the pterygoid in the manner already described. At its lateral limit is the orifice of a canal which penetrates the bone obliquely. This canal appears to be formed by the rolling over of the mesal margin of the bone to meet a similar process arising from the surface. The two enclose a short canal which terminates in a fissure which extends to the apex of the bone. This blind canal and fissure probably represent the lachrymal canal of other mammals.

It has been said that this mesal extension of the lachrymal terminates in a vertical edge. This can be seen from the nasal fossa in a fissure between maxilla, palate, and pterygoid on the one hand, and frontal on the other. In the articulated state, it appears to establish contact with the tip of that dorsal extension of the vomer described as the sphenoidal turbinal. The process as a whole lies in a bed formed for it by the maxilla, palate, pterygoid, and frontal.

The Jugal.—The jugal is a small bone possessing a three-sided body and a long slender shaft. The dorsal surface is convex in its transverse diameter and quadrilateral in outline, though the lateral border is so short as to make the surface approach a triangle. This surface articulates with a similarly shaped area on the ventral surface of the maxilla. The lateral border projects beyond the border of the maxilla in the antorbital notch.

The caudal surface is deeply concave in all dimensions and triangular in shape, the base of the triangle being placed laterad, the apex being prolonged into a slender process mesad. This surface fits like a cap over the convex cranial surface of the lachrymal bone, the slender process mentioned being received into a deep depression between lachrymal and maxilla.

The ventral surface is irregularly triangular in outline, the apex of the triangle being formed by that slender process which fits in between lachrymal and maxilla. The surface, where prolonged on this process, is, in the articulated state, overlapped by a ridge of the maxilla. The rest of the surface is free on the ventral surface of the base of the rostrum. From the ventral surface rises by a broad flat base the zygomatic process. This is a round, slender shaft of bone which reaches caudolateral almost to the tip of the jugal process of the frontal.

Squamosal.—The squamosal is notable for the massive process which supports the glenoid fossa and zygoma, contrasted with the insignificant plate which lies in the wall of the cranium. This latter is oval in outline, concave on its ental surface and convex ectally. The whole ental surface articulates with a tongue-shaped area on the outer surface of the parietal. The dorsal half of the circumference of this section is very thin and fades into the ectal surface of the cranium. The caudal portion of the ventral half of the border presents a hook-like projection which is received into a recession on the ventral border of the jugular process of the exoccipital.

The rostral portion of the ventral half of the border articulates by means of a wide grooved surface with the lateral border and inferior surface of the processes ascendens of the alisphenoid. Between these two articulations, that with the alisphenoid and that with the exoccipital, the ventral edge of the squamosal plate forms a free edge indented by a deep notch which borders on the foramen lacerum medium and assists in forming the bed of the periotic bone.

The glenoid process is a strong, quadrilateral mass of bone attached by its mesal border to the ectal surface of the squamosal plate. It is placed with its rostral border in a more dorsal plane than the caudal and its surfaces thus face rostroventrad and dorsocaudad. The dorsal surface is, for the greater part of its extent, convex and shows roughening for the attachment of muscles.

The ventral surface forms the glenoid fossa. This is quadrilateral in outline and markedly concave in all dimensions, owing to the decurvation of all the borders, especially the lateral. A well marked zygomatic process terminates the lateral border rostrally and a less massive postglenoid process is present caudally. Between the two, the border is deeply concave. The mesal border falls into two divisions. The rostral forms a thin margin, which is just under the ala temporalis. The caudal division forms a free, concave, sharp margin, which terminates at either end in a point. From the rostral of these springs a crescentic finger-like process, which curls about the anterior mass of the periotic bone. The whole free margin, which is known as the falciform process, in the articulated state lies under the periotic and holds it firmly in place.

The surface of the glenoid fossa is smooth rostrally but rough approaching the caudal border, possibly to afford attachment to the articular cartilage.

A third process juts caudad from the junction of the squamosal and glenoid portions of the squamous bone, giving it a triradiate appearance on lateral view. This is a pyramidal, hook-like structure which fills in the space between the glenoid mass and the exoccipital. Its ectal surface is continuous with those of the squamosal plate and glenoid process. Its ental surface assists in forming the lateral wall of the periotic bed. Its third surface articulates with the exoccipital.

This process becomes greatly thickened in the adult skull and forms, with the exoccipital, a notch which receives the tympanomastoid. Between it and the caudal edge of the glenoid process is a distinct groove for the external auditory canal.

The Palate.—The palate, a flat scale of bone, is placed at the base of the rostrum on the lateral surface of the maxilla. Two portions may be distinguished: an anterior, thin and broad, which lies compressed between

maxilla and pterygoid; and a posterior, massive and irregular, set at an angle to the first.

The lateral surface of the anterior portion shows a dorsal region, flat and smooth, which appears on the ventral surface of the rostrum, extending a little cranial to the pterygoid. Ventrad to this, separated from it by a ridge, is a broader portion, longitudinally striated, which in the articulated skull is overlain by the pterygoid. The mesal surface of this division is opposed in almost its entire extent to the ectal surface of the maxilla. The caudal extremity of the ventral border, however, forms a small projecting spur which overrides the maxilla and articulates with the vomer. The midline of this surface is marked by a groove for the posterior palatine canal.

The caudal portion of the bone, though narrow, is much thicker than the rostral and forms an angle therewith, changing direction mesad to fit the convexity of the maxilla. The dorsal border at the junction of the two sections shows a deep, smooth-edged groove which forms the inferior margin of the proximal opening of the maxillary foramen. Caudad to this is a thin, tongue-like projection, with a concave ectal surface, which lies in the inner wall of the lateral maxillary foramen. The extremity of the process presents a sharp edge, which overrides rostrad and excludes the tip of the sphenoidal turbinal from the nasal fossa.

The ventral margin of the caudal process of the palate is a sharp crest which fits into a groove on the inner surface of the pterygoid, aiding to form a firm union with that bone. The mesal margin is also prominent and fits under a ledge on the ventrocaudal surface of the maxilla. Three surfaces are included between these borders. The ectal shows a small area rostrad in a gap between lachrymal and pterygoid which lies in the floor of the sphenomaxillary fossa. This section is grooved by a canal which comes through the bone from the nasal passage, probably the sphenopalatine canal. A second canal formed between lachrymal and palate bone, divided from the one already mentioned by a thin partition, also enters this space from the nasal fossa. The remaining caudal portion of this surface is divided between a dorsal smaller area for articulation with the lachrymal and a larger ventral area for articulation with the pterygoid.

The mesal surface is smooth, concave rostrocaudally, narrow, and forms a portion of the lateral wall of the nasal passage, appearing between maxilla and pterygoid. The dorsal surface shows several longitudinal elevations and depressions which correspond to irregularities of the maxillary surface with which it articulates.

BONES OF THE FLOOR OF THE CRANIUM

Basioccipital.—The basioccipital presents for description a body and paired basal processes.

The body forms the floor of the posterior fossa of the skull. It is divisible into two portions, a cranial quadrilateral area which is firmly fused to the basisphenoid and bears on its lateral borders the basioccipital processes, and a caudal triangular area. This latter portion lies with its base craniad and apex caudad on the foramen magnum, firmly wedged between the exoccipitals. It is demarcated from the former by lateral notches which suggest a previous complete separation.

The ental surface of the body, owing to the elevation of its borders is concave in all directions. Low marginal ridges serve to delimit it from the basisphenoid and basal processes, the superficial aspect of the bones being homogeneous. Near the apex of the triangular portion, bordering on the foramen magnum, there is a slight falling away of the surface, rendering this portion convex.

The ectal surface of the body is flat longitudinally and deeply concave transversely, owing to the extension ventrad of the basal processes. The caudal half of the triangular portion is roughened and divided into central and lateral areas by parallel, longitudinal fissures. The lateral areas, in the articulated state, form part of the surfaces of the condyles for articulation with the atlas. The central area, of which there is no indication in the adult, appears to form part of the general articular area and strongly suggests that in the young of this animal there may be a single horseshoe-shaped joint which becomes divided in later life.

As concerns the borders of the basioccipital, the cranial, as mentioned above, is firmly fused to the basisphenoid. The lateral borders give origin for their cranial one-third to the basioccipital processes. The caudal two-thirds present a wide roughed area for articulation with the exoccipital.

The basioccipital processes arise from the anterior one-third of each margin of the basioccipital, a low broad ridge on the dorsum marking the point of origin. Laterad to the ridge, there is a slight falling away of the surface. This section of the bone is narrow and almost directly horizontal. An inch from its origin the process turns ventrad, at the same time undergoing a considerable anteroposterior expansion. There is thus formed a vertical plate of bone, the surfaces of which, owing to rotation on a vertical axis, present laterocraniad and mesocaudad.

A transverse fissure separates the horizontal portion of the process from the caudal edge of the alisphenoid. At the point where the process bends

ventrad, the fissure turns over the lateral border of the skull base between alisphenoid and basioccipital processes. After a short extension downward, it passes forward and inward between the ectopterygoid ridge of the basisphenoid and the cranial extension of the basal process. Thus the latter process presents the appearance of a sickle, the handle joining the basioccipital, the blade hooking forward and inward around the ectopterygoid ridge. The fissures do not extend through the bone to the ventral aspect, so that this view does not show the limits of the structures mentioned.

The dorsal surface of the horizontal portion of the basal process is marked by a prominent transverse ridge. In the articulated state, this extends towards a similar protrusion on the ental surface of the exoccipital, the two partially dividing the foramen lacerum into caudal and cranial divisions.

The cranial border of the basal process lies against the inner portion of the alisphenoid, the line being marked, as above described, by a fissure. The vertical plate has a dorsal border, hooking about the ectopterygoid, and a caudal border, which articulates in nearly its whole extent with the exoccipital. Near the tip, this border is free and is separated from the paracondyloid process of the exoccipital by a deep notch at the bottom of which opens the hypoglossal foramen.

In the articulated skull, the basal processes form a considerable portion of the paired, great longitudinal ridges which extend from the base of the rostrum cranially to the exoccipitals, caudally fitting between pterygoids and the paracondyloid processes of the exoccipitals.

The Sphenoid.—The sphenoid consists of a central portion, the basisphenoid and paired lateral processes, the alisphenoids.

The basisphenoid is a quadrilateral mass of bone which lies in the floor of the middle fossa of the skull. Caudally, it is firmly fused to the basioccipital. Cranially, fusion with the presphenoid has not yet occurred. The alisphenoids are firmly attached to the lateral borders of the body, though careful examination reveals certain lines of demarcation.

The ental surface of the body shows a well-marked transverse ridge, which may be identified as the dorsum sellæ. Anterior to this ridge is a shallow depression corresponding to the sella turcica of other mammals. The floor of this fossa is perforated by a small canal which reaches the ventral surface of the bone, evidently the canal for the hypophyseal stalk. Craniad to the sella, the surface of the bone is elevated in the midline by a rough ridge which mounts to an elevated margin along the border of the bone. On each side of the central ridge, the bone is longitudinally grooved by channels for the internal carotid arteries.

The ventral surface of the basisphenoid is concave transversely. In the midline can be seen the inferior opening of the hypophyseal canal.

The caudal border of the basisphenoid is fused, without line of demarcation, to the basioccipital. The cranial border presents a rough quadrilateral area, longest transversely, which articulates with the presphenoid. To the lateral margins are united the alisphenoids.

The alisphenoids consist of two portions: a mesal, which is in close relation to the body; and a lateral, or processus ascendens. The mesal, or processus alaris, is an oblong block of bone united by one long border to the basisphenoid. The line of union is marked at the junction of the middle and anterior thirds by the carotid foramen, which penetrates the bone from the ectal surface craniomesad. Grooves proceed both craniad and caudad from the foramen. The cranial of these reaches the anterior border of the bone and is evidently the external expression of the fissure which shows on the cross section and almost separates basi- from alisphenoid though not reaching the surface. The caudal of the two grooves leading from the carotid foramen reaches halfway to the posterior border, where it ends in a small excavation seemingly the remains of a canal which at one time deeply penetrated the bone. Both these grooves are probably occupied by vessels.

The fissure delimiting the basioccipital process from the alisphenoid has been described. At the point where it turns over the margin of the bone, an additional fissure branches from it. This passes forward, gradually increasing its distance from the former until it reaches the ectal opening of the carotid canal. The two fissures include between them a narrow, triangular strip of bone which lies with its base on the basisphenoid rostrad to the cranial margin of the basal process of the basioccipital. This portion of bone I take to represent the ectopterygoid process of the basisphenoid.

The dorsal surface of the processus alaris, craniad to the carotid foramen, is flat and passes smoothly on to the surface of the basisphenoid. Caudad to the carotid foramen, the surface becomes high and convex, owing to the presence of a prominent tubercle on the lateral border to be described later. The ventral surface is rough and convex longitudinally.

The cranial border of the processus alaris is short and articulates with a process from the presphenoid. The caudal border rests against the basal process of the basisphenoid. The union of the mesal border to the basisphenoid has been described. The lateral border demands more extended mention. Cranially, it gives origin to the processus ascendens. The line union is marked by a dorsal groove which leads from a notch in the caudal edge of the root of the processus. Caudad to this notch, the border juts laterad to form a prominent tubercle which in its turn is limited caudad by another deep recession. This latter borders on the foramen lacerum and is included in the caudal division of that opening. The tubercle helps to

separate the foramen lacerum posterior from the region of the foramen lacerum medium.

The processus ascendens takes origin from the anterolateral angle of the processus alaris by a narrow, flattened bar of bone. This passes for a short distance laterocranially, and then expands into a thick, quadrilateral block. The upper surface of this mass is marked mesally by a groove which probably provides passage for the middle meningeal vessel. Laterad to the groove is a broad smooth area which, in the articulated skull, is overlain by a process of the parietal bone. Cranially, there is a narrow, fissured area for articulation with the frontal bone.

The ventral surface is divided by a well-marked groove into a rostral smooth area, which borders on the sphenoidal fissure, and a caudal roughened area, which articulates in its whole extent with the squamosal. Laterally, there is a narrow border, which articulates with the frontal bone. The groove is for the third branch of the fifth cranial nerve.

The anteromesal border of this section is smooth and sharp, and bounds on the sphenoidal fissure. The anterolateral border is sharp and wedged-shaped for articulation with the frontal. The posterolateral border is divided into two narrow longitudinal strips, the ventral of which articulates with the squamosal, the dorsal with the parietal bone. The posteromesal lies on the foramen lacerum. It presents two indentations, a lateral for the middle meningeal vessel and a mesal for the third division of the fifth nerve.

BONES OF THE BRAIN CASE

The Supraoccipital.—The supraoccipital enters into the formation of a considerable part of the caudal wall and roof of the cranial vault. Its borders are exceedingly irregular. Lying on the foramen magnum is a short, concave area occupying one-fourth of the circumference of that opening. This margin is thin and sharp. On either side of the foraminal area the bone becomes thicker and presents on cross section a fairly broad, semi-oval articular surface for the exoccipital. This portion becomes narrow laterad and is succeeded by an exceedingly thick indented area which borders on the lateral occipital fontanelle. For the remaining half of the distance to the lateral angle of the bone the margin is rough and is dissimilar on the two sides, owing to irregularity of the disarticulation. Close examination shows that the parietals jut under the supraoccipital to a considerable extent and have, in a varying degree, remained attached to that bone.

From the lateral to the cranial angle there is a smoothly concave border of gradually increasing width which is slightly striated. This articulates

with the frontal. In the midline is an area, in length one-fifth the breadth of the bone, which is straight transversely. This is delimited from the concave section on each side by an angle. The surface here is of considerable width and deeply concave in all dimensions. Each half of this area receives a prominence on the border of the corresponding frontal, firm union being thus secured.

It has been mentioned that a considerable portion of the parietal on each side, overridden by the supraoccipital, has remained attached to this latter. Along the border, from the lateral to the cranial angle, there is a very narrow margin of bone which seems separated from the supraoccipital by a shallow fissure on the ectal surface and to belong with the parietals. In the midline, also, a considerable section of the supraoccipital crest is partially delimited by fissures from both supraoccipital and parietals. These fissures appear to indicate previous complete separation and so the presence of parietals reaching almost the midline and the presence of an interparietal between them.

The ectal surface shows a central depressed area passing caudocranially, taking in the whole width of the bone at the caudal angle. This corresponds to the supraoccipital crest on the ental surface. On either side of the central concavity is an elevated, uniform convexity, the external indication of the internal hollows which receive the cerebral lobes.

The ental surface is marked by a high supraoccipital crest with a deep uniform concavity on either side. This supraoccipital crest passes cranio-caudad from the cranial angle of the bone to within a short distance of the inferior angle. Here it bifurcates and the two resulting crests pass laterad to the center of the broad articular areas for the exoccipitals. These latter are continuations of similar crests on the ental surface of the exoccipitals and furnish attachment to the tentorium. The central crest itself is probably due to ossification of the falx cerebri and aids greatly in reinforcing the skull vault against anteroposterior pressure. It has already been mentioned that a considerable portion of the crest, in its most cranial region, is partially marked off from the rest by fissure and the suggestion was made that this area might represent an interparietal bone. This part is further subdivided by a fissure showing on only one side, and so there may be present here pre-interparietals as well as interparietals.

Exoccipital.—The exoccipital is roughly quadrilateral in shape, having two mesal and two lateral borders. The bone varies greatly in thickness, being massive at the ventromesal border, thin and shell-like at the dorso-lateral. The ventromesal border presents an extensive articular surface for the basioccipital. This falls into two divisions, separated by an obtuse angulation and a small fissure. The dorsal is the broader of the two, as

the bone is there thickened for the formation of the condyle on the ectal surface. The ventral is of uniform width and slightly concave. The inferior one-third of this area is born on a spur of bone which limits mesally the hypoglossal notch, the outer limit being the paracondyloid process. In the articulated condition this angulated border fits into a corresponding reentrant angle of the basioccipital, the fissure and concavity of the ventral area at the same time receiving a protrusion from the basioccipital. There is thus formed a firm interlocking joint.

The ventral half of the dorsomesal border is concave and sharp and enters into the margin of the foramen magnum. Dorsally, the border turns craniad and forms an articular surface of gradually diminishing breadth for the supraoccipital.

The dorsolateral border is a thin, sharp margin of irregular outline which helps to limit the lateral occipital frontanelle. The ventrolateral border is also thin, of sinuous outline, and protrudes to a slight extent ectally, thus assisting in the formation of a salient ridge at the occipitosquamosal suture.

The ental surface of the exoccipital is exceedingly uneven. From the angle at the centre of the ventromesal border there curves dorsal a well-marked, rounded ridge which meets the dorsomesal border just above the limit of the indentation of the foramen magnum. This is continuous with a similar ridge on the ental surface of the supraoccipital and evidently affords attachment to the tentorium. Caudad to this ridge, the surface of the bone is concave to form part of the posterior fossa for the lodgement of the cerebellum. In this concavity appears the ental opening of the hypoglossal foramen. This canal passes through the bone cranioventrad to its ectal outlet in the hypoglossal notch between basi- and exoccipital. Cranial to the ridge is a triangular concave surface which enters into the side wall of the middle cerebral fossa. This is limited ventrally by a massive projection of bone of triangular base and double apex. The dorsal surface of this mass presents in the cranial cavity. The anterior surface is extracranial, being covered in the articulated skull by the parietal. Ventral to the surface of the parietal is a deep depression which receives a spur from the squamosal, thus forming a dovetailed articulation.

The ventral surface of the exoccipital spine is extracranial and helps form the bed for the periotic capsule. Of the angles delimiting the surfaces of the pyramid, the dorsal is a smooth even ridge which fades gradually into the surface of the bone. The ventral is rough, broad, and overlain nearly to the apex by a protuberance of the squamosal. The caudal is marked about midway by a sharp spur which gives the pyramid the appearance of having a double apex. This spur projects toward a similar one on the basioccipital and the two almost divide the foramen lacerum posterum

into caudal and cranial divisions. The larger apex reaches toward the commissura aliochlearis of the alisphenoid and with this indicates the cranial limit of the foramen lacerum posterium. The whole mass corresponds to the processus jugularis of other mammalian skulls. Below the jugular process is a smooth concave surface which forms the ventral aspect of the paracondyloid process. This is covered along its lateral margin by the squamosal. The remainder of the surface is free and forms the caudal wall of the periotic bed.

The ectal surface of the exoccipital reveals three elevations separated by a Y-shaped depression. Caudally, at the junction of the mesal surfaces, is a rough, crescentic elevation which forms the larger part of the condylar articular surface of one side. Ventrally, beneath the cranial arm of the Y, is the smooth, convex ectal surface of paracondyloid process. Dorsally, between the arms of the Y, is a low wide elevation which is the external expression of the concavity which lodges the posterior lobe of the cerebrum.

Frontal.—The vertical portion of the frontal, in union with its fellow of the opposite side, forms a large part of the rostral wall of the skull cavity. It has the shape of one-quarter of a circular disk, with the straight borders mesad and ventrad. Centrally, the bone is thin and comparatively fragile. The entire circumference is thickened, especially the dorsal and ventral margins. The former of these expands mesally into a massive process which forms, when articulated, the prominent vertex of the cranium and furnishes broad surfaces for articulations. The latter gives rise rostrally to the orbital process and caudally to a thick projection which embraces the tip of the ala orbitalis and articulates with the greater wing of the sphenoid.

The caudal surface is, for the most part, uniformly concave. The dorsomesal angle, however, is occupied by a considerable triangular area, broad mesad, pointed lateral, which is roughened, convex dorsoventrad, and articulates with the supraoccipital. The ventral part of the lateral border also presents a smaller triangular area for articulation with the parietal.

The rostral surface is centrally convex in correspondence to the concavity of the ental surface. In the dorsal and ventral regions, owing to the thickening of the bone, the surface becomes concave. Below, it passes smoothly on to the dorsal surface of the orbital process. Near the lateral border is a narrow strip marked off from the general surface by a shallow groove, above by a low ridge. This represents an area which appears as a free border in the articulated state. The remainder of the surface is opposed to the frontal portion of the maxilla on articulation, the two thus forming a double vertical front wall for the skull. The lateral and dorsal borders take part in the formation of the great transverse crest. The mesal border

is considerably thickened. At the dorsal termination is a triangular area for articulation with the nasal bone. Ventral to this succeeds a smaller surface which meets the frontal bone of the opposite side. The lower half of the border is bevelled at the expense of the rostral surface. This bevelled area presents a thin, sharp edge mesad, which borders on the frontal fontanella. The surface itself is very rough for the attachment of ligaments. The ventral margin, however, furnishes a narrow strip of smoother aspect for articulation with lachrymal, laterad, and pterygoid and sphenoidal turbinal, mesad.

The orbital process is a triangular projection of the rostral aspect of inferior margin of the vertical portion. Its apex points ventromesad and rostrad. The lateral border is continuous with that of the vertical portion and the dorsal surface here presents a narrow strip marked off by a shallow groove. The mesal border is concave, moderately sharp, and articulates for its whole length with the lachrymal, into a depression of which it fits.

The dorsal surface is concave caudorostrad and is covered in the articulated state by the maxilla. The ventral surface is slightly concave in all dimensions, and forms the main part of the roof of the orbit.

The postorbital process rises from the junction of the lateral borders of the vertical and orbital portions. It is a sharp spur which points caudolateral. Its mesal surface is smooth and concave and limits the temporal fossa laterad. The ectal surface is convex and rough.

A thick three-sided protuberance projects caudoventrad from the caudal aspect of the junction of orbital and vertical processes. The upper surface of this structure faces in the cranial cavity. The inferior surface partially roofs in the temporal fossa. The mesal surface is deeply indented by a narrow groove which, in the articulated state, forms the outer extremity of the sphenoidal fissure. Of the borders, the outer presents a narrow articular surface for the parietal continuous with that on the dorsal surface of the vertical division. The caudal border is deeply striated for articulation with the ala temporalis, and the mesal concave margin receives the blunt, lateral extremity of the ala orbitalis. The lower lip of the groove on the mesal surface articulates with the palate.

Presphenoid.—The presphenoid, in its extension from basisphenoid to mesethmoid, rises more and more sharply so that it enters not only into the floor of the cranial cavity, but into the anterior wall as well. It is as yet separated from the basisphenoid by an open fissure. The ala orbitalis and mesethmoid are, on the other hand, already firmly united to it and the delimiting lines are with difficulty made out.

The sphenoidal body is a quadrilateral mass of considerable thickness. Its ental surface is uniformly concave in the sagittal axis, the rostral border

being placed at a much higher level than the caudal. Thus the surface as a whole looks dorsocaudad, the rostral region almost directly caudad. The midline is occupied by a low, wide, longitudinal ridge. This is the surface expression of the base of the mesethmoid which is deeply set into the bone from the ventral aspect. Owing to the presence of this ridge, the surface is concavoconvex in its transverse aspect. As a whole, it forms a broad shallow depression for the optic chiasm and laterally the optic nerves.

The ectal surface of the sphenoidal body is markedly convex in all dimensions, bevelling at its expense occurring in the lateral and rostral regions. In the midline, the thick mesethmoid juts rostrad. The lateral regions are, in the articulated condition, concealed from view by the sphenoidal turbinals and vomer mesally and by the pterygoids along the borders.

The rostral margin is sharp and on each side falls away laterad where it demarcates the orbitonasal fissure. In the midline it lies against the mesethmoid and, though the union is close, a transverse line of fusion can be made out.

The caudal border articulates with the basisphenoid. At its lateral limits fissures of considerable depth indicate the original separation of the ala from the body. In the midline, the cross section shows an inverted V-shaped depression which rests its limbs on the ventral margin of the border and extends its apex almost to the dorsal surface. This may be taken to indicate the original separation of the part included in the V, the base of the mesethmoid, from the main mass of the sphenoidal body wherewith it forms a morticed union.

The lateral borders bear the alæ orbitales. Two areas can be distinguished in these structures. Springing directly from the sphenoidal body is a triangular process sloping caudorostrad. The upper surface is concave, broad at its origin, but narrow laterad till it terminates in a spout-like process which forms the ventral half of the circumference of the optic foramen. This triangular process corresponds to the structure found in the chondrocrania of other mammals designated as the ala hypochiasmatica (Voit). It has been shown to chondrify independently of the presphenoid and so the separate ossification here indicated can be understood.

From the extremity of the ala hypochiasmatica rises the ala orbitalis proper by two pedicles which unite to form an arch over the optic foramen. Of these pedicles the caudal is much the more slender and it appears to extend itself along the caudal border of the ala hypochiasmatica to the body itself of the presphenoid, becoming incorporated in the region cut off by that fissure on the caudal border already mentioned. Here is formed a short process seemingly continuous with the root of the ala orbitalis, which extends caudad to the border of the sphenoidal body and articulates with a special process of the basisphenoid.

The rostral root of the ala orbitalis is thicker and almost vertical in position. It takes its origin by a triangular base but quickly loses this shape through the flattening of one of the angles. At their junction, the roots form a flat bar of bone with dorsomesal and ventrolateral surfaces and narrow borders.

It will be seen that the whole ala orbitalis proper consists of the arch enclosing the optic foramen out of all proportion smaller than the ala hypochiasmatica.

The ala orbitalis appears at the mesal extremity of the orbit, encircled by frontal, lachrymal, and pterygoid. Of these bones with only the frontal does it form an articulation. This is by the periphery of the arch. The articular surface is broad rostrad, being one of the surfaces of the triangular base. It quickly narrows and maintains a uniform width to the caudal limit of the articulation. From this point a narrow border passes mesocaudad to join the border of the ala hypochiasmatica at an acute angle. This margin is the dorsal limit of the sphenoidal fissure.

Nasals.—The nasal bones, owing to their close approximation and firm union, really form an entity. This consists of a three-sided pyramidal mass which rests its base against the frontals, the caudal portions of its sides between maxillæ and premaxillæ, and which overhangs with its prow-like ventral surface and apex the nasal cavities. The dorsal surface of the mass forms the summit of the transverse crest. The bone of the left side is considerably smaller than that of the right, which overreaches it dorsad and caudad. On the other hand, the ventral extension of the left is greater than that of its fellow. Four surfaces and a base may be distinguished in each bone.

The base rests against the rostral face of the summit of the frontal. It is a slightly concave surface which faces laterad as well as caudad owing to the marked caudal production of the mesal border. That of the right extends beyond the caudal border of the left and thrusts itself between the two frontals. Thus the right nasal bone articulates with both of these bones; the left only with that of its own side. The whole base of the right nasal articulates with the frontal of its own side. On the other hand, the lower portion of the base of the left is refused so that only the upper half of the surface enters into this articulation in the case of this bone. Across the middle of this surface of the left bone passes a transverse groove which joins a canal between the two bones channelling their respective mesal surfaces.

The dorsal surface is triangular, smooth, convex antero-posteriorly. That of the right is more extensive in all dimensions and rises higher than that of the left. Together, the two bones form a wedge with its apex rostrad between the nares.

The lateral surface is triangularly convex and, owing to bevelling at the expense of its ventral margin, looks slightly ventrad. A small articular surface for the premaxilla exists along the caudal margin of this aspect of each bone. The rest of the surface is free.

The mesal surface is convex on the right bone, concave on the left, the two being thus neatly adapted to one another. That of the right side is prolonged caudad beyond the left and articulates with the left frontal, as already mentioned.

The ventral surfaces differ considerably on the two sides. That of the left forms a triangle with the base caudad. The caudolateral angle is produced downward in the form of a spur, rendering the surface immediately rostrad concave. The mesal border is slightly elevated and with a similar formation on the right bone forms a central caudorostral ridge on the ventral aspect of the nasal bone complex. The lateral border has a lateromesad direction, owing to the bevelling of the outer surface which affects chiefly the rostral region.

The ventral surface of the right presents two triangles, base to base, their apices rostrad and caudad. The first, except for being somewhat broader, corresponds to the ventral surface of the left nasal. The second represents the ventral surface of that caudal extension of the mesal border of the base of the bone already described. It is concave transversely, convex caudoventrad, owing to the refusal dorsad of the apex.

Ethmoid.—The mesethmoid is a triangular plate of bone which rests its base in the dorsal groove of the vomer, and extends its apex high into the ethmoidal notch between the frontals. The base is markedly convex transversely, straight caudorostrad and thickened at either extremity.

The rostral border leaves the ventral at an acute angle and extends dorso-caudad. It is convex longitudinally, plane from side to side, and extensively pitted to afford attachment to the septal cartilage. The cross-section shows the bone to be of soft porous structure.

The caudal border, for the greater part of its extent, is buried in the rostral face of the presphenoid. The dorsal extremity, however, rises above that structure for about half an inch, meeting the rostral border at an acute angle and forming a prominence which corresponds to the crista galli of other mammals. This border is concave to coapt it to the convex rostral surface of the presphenoid, and like the rostral, is considerably thicker near its ventral limit.

The lateral surfaces of the mesethmoid form the mesal walls of the nasal passages. They are slightly convex in the vertical direction, concave caudorostrad. Along the ventral and caudal margins they are overlain respectively by the vomer and ectethmoids. These latter bones so closely fuse to the surface that their limits can be made out only approximately.

The dorsal view shows that the bone has a distinct twist to the left, especially approaching the upper margin. The rostral tip, on the other hand, twists to the right, rendering the right lateral surface more deeply concave than the left. This deflection falls in with the general asymmetry of the skull in the narial region.

The lateral ethmoid regions consist of paired thin plates of bone attached by their mesal margins to the mesethmoid in the region of the crista galli. As they extend laterad their surfaces look toward caudad and rostrad and their lateral borders are lapped rostrad by the mesal margins of the sphenoidal turbinals. From the rostral surface of these plates thin projections which enclose between them the mesethmoid extend forward. These terminate in sharp edges which lie close to the surface of that bone, the line of demarcation being scarcely distinguishable. They present a concave, smooth surface to the nasal cavity, and a plane surface to the mesethmoid, from which they are separated by a narrow fissure. Into this fissure there opens from the cranial cavity a narrow crack, which is thought to allow passage to the nasal branch of the first division of the fifth cranial nerve. These lateral extensions of the mesethmoid are interpreted as representing the turbinals and accessory air spaces of other mammals. The space enclosed by them is the ethmoidal region. (Compare with De Burlet's work.)

Parietal.—The parietal is a shell-like bone, concave entally, convex ectally, which fits in the side wall of the cranium like a wedge between the converging frontal and exoccipital. It rests its thick base on the dorsal aspect of the alisphenoid. The thin pointed tip is overridden dorsally by the exoccipital. The anterior border, becoming thinner ventrodorsad, articulates in its whole extent with the frontal. Its caudal border articulates from its ventral one-third by a broad convex surface with the jugular protuberance of the exoccipital. The ental surface lies, in part, free on the outer aspect of the cranium. The ventral one-third of this surface is occupied by a depressed tongue-shaped area for articulation with the squamosal, which overlies it.

THE MANDIBLE

The mandible is an elongated bone, broad and thin caudally, more massive but narrow towards its rostral tip. It undergoes, caudorostrad, a rotation in its long axis, so that, whereas the broader surfaces lie in the vertical plane, the narrow distal surfaces slope from below mesolaterad. Its proximal extremity bears the condyle for articulation with the glenoid cavity. The pointed distal extremity presents a cylindrical excavation for a tooth.

As mentioned above, the proximal half of the bone is broad and thin, gradually narrowing rostrad. The external surface is convex, the summit of the convexity being angular and somewhat nearer the dorsal than the ventral border. Along the line of this angulation the bone is considerably thickened. Toward either border it becomes thinner and the margins are sharp. The thickening affords considerable increase in the structural strength of the bone. The internal surface in this region presents a broad fossa, open in nearly its whole extent. Approaching the narrower portion of the bone, however, the borders give origin to shelving projections which tend to deck over the fossa more and more till they meet at an acute angle. Thence rostrad for a short distance is a complete cylinder of bone enclosing a canal which communicated rostrally with the dental groove.

The change in the width of the bone at the center of its longitudinal extent is abrupt, the full degree of narrowing being quickly reached. Thence forward to the region of the symphysis the breadth is uniform. The external surface continues rostrad in an even more marked degree the ridge found more caudally. This ridge finds its termination at a point opposite the proximal end of the symphysis, where it disappears. Just ventrad to this termination is a large mental foramen. The rostral continuation of the surface is concave caudo-rostrad, convex dorsoventrad, and faces slightly ventrad owing to the rotation of the bone already mentioned. The surface markings of this region are of interest. Strands of the most dense structure radiate from a point on the axial ridge near its center, rostrad, dorsad, and caudad. This formation would appear to be designed to make up in this situation the strength otherwise lost through its greater narrowness as contrasted with the region immediately caudad.

The internal surface of the narrow portion is smooth throughout the greater part of its extent and convex dorsoventrad. The rostral one-third, however, is set off from the rest by a prominent ledge which passes obliquely dorsoventrad and caudad. This area, of elongated oval shape and longitudinally striated, joins the bone of the opposite side in the symphysis.

The dorsal border of the mandible in the caudal half is slightly concave. In the middle of its course it passes over a slight convexity, then falls away ventrad, thus giving rise to the narrowing of the bone. To the middle of the symphysis the margin is then horizontal. At this point it turns dorsad and, as the ventral border follows, the termination of the bone has a marked upward turn. In the caudal half the edge is smooth and rather sharp. The rostral half is channeled by an alveolar gutter which deepens till it almost splits the bone. It terminates at its very extremity in a large, round, tooth socket.

The inferior border of the mandible is uniformly concave from the caudal

extremity to the middle of the symphysis. Here it turns dorsad, in correspondence to the dorsal border, and becomes markedly convex.

From the lateral view the bone as a whole has a sinuous outline, being horizontal in its caudal half then turning slightly ventrad till the symphysis is reached when it turns dorsad. This appearance is entirely due to the direction of the borders. The axial ridge is straight and horizontal from its caudal termination in the condyle to its rostral termination at the symphysis.

The rostral extremity of the mandible is blunt and is perforated by the round tooth socket. The caudal extremity is convex in its general outline. Two-fifths of its extent, somewhat nearer the dorsal than ventral margin, bears the condyle. This projects a short distance beyond the rest of the margin and presents an oval facet, roughened for union with the articular cartilage. This condyle, in reality, is the caudal extremity of the axial ridge of the whole bone whose cross-section it represents.

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 1880, Proc. Zool. Soc. London, p. 232;
 1883, Proc. Zool. Soc. London, p. 590.

EXPLANATION OF PLATES

PLATE XX

- Figure 1. Dorsal view of adult female skull.
 Figure 2. Ventral view of adult female skull.

PLATE XXI

- Figure 1. Dorsal view of foetal skull.
 Figure 2. Ventral view of rostrum, foetal.

PLATE XXII

- Figure 1. Lateral view of adult skull.
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PLATE XXIII

- Figure 1. Floor of cranial cavity, foetal.
 Figure 2. Rostral wall of cranial cavity, foetal.

PLATE XXIV

- Figure 1. Caudal wall of cranial cavity, foetal.
 Figure 2. Lateral wall of cranial cavity, foetal.

PLATE XXV

- Figure 1. Basi- and exoccipitals, ental aspect, foetal.
 Figure 2. Basi- and exoccipitals, ectal aspect, foetal.

PLATE XXVI

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PLATE XXVII

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PLATE XXVIII

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Mesal aspect, right premaxilla (below).

PLATE XXIX

- Figure 1. Dorsum of vomer, mesethmoid, and presphenoid.
Figure 2. Lateral aspect of vomer, mesethmoid, and presphenoid.
Figure 3. Ventral aspect of vomer, mesethmoid, and presphenoid.

PLATE XXX

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Figure 2. Palate and lachrymal bones.

PLATE XXXI

- Figure 1. Pterygoids.
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PLATE XXXII

- Figure 1. Mandible.
Figure 2. Frontal.

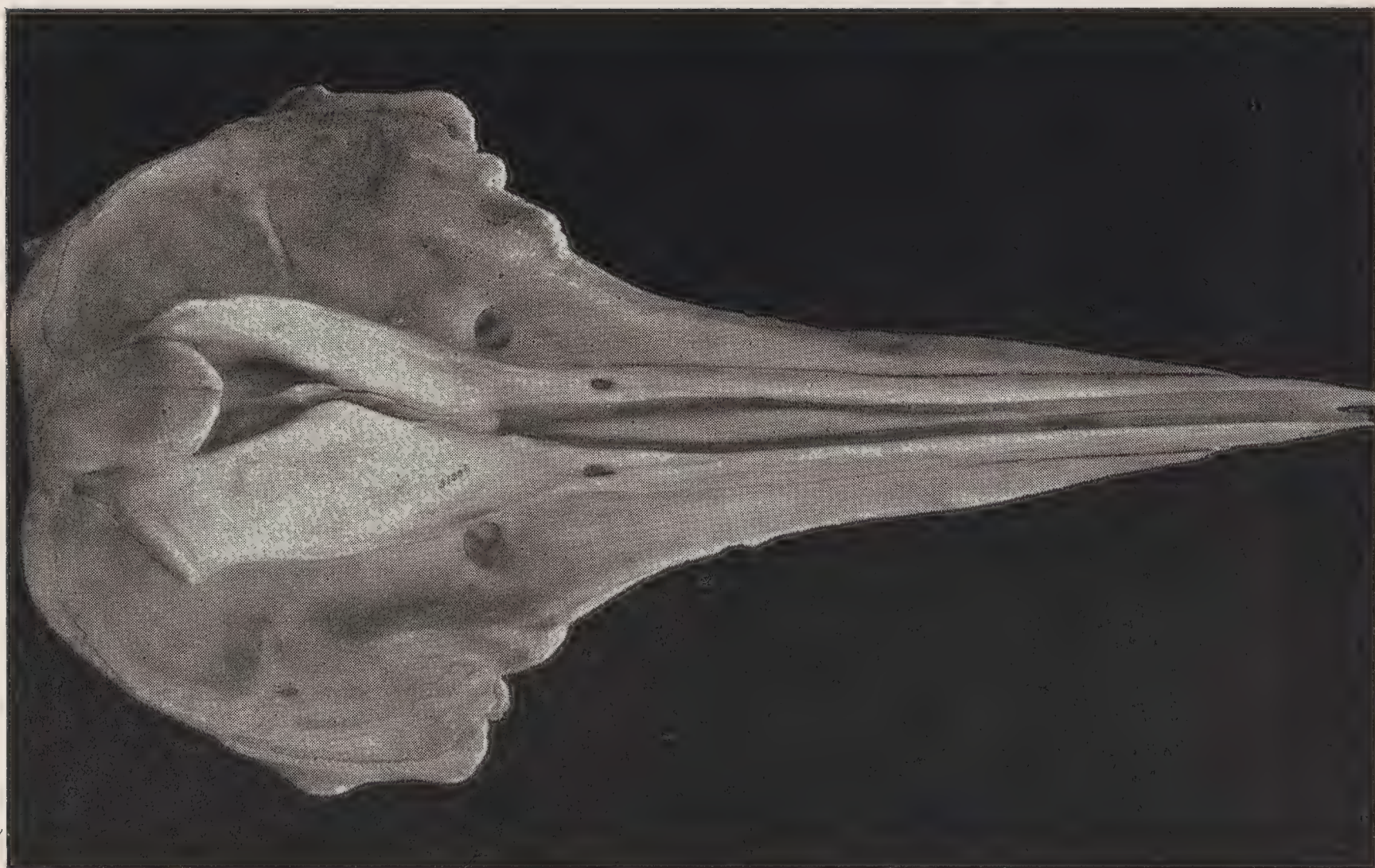


Fig. 1. Dorsal view of adult female skull.



Fig. 2. Ventral view of adult female skull.



Fig. 1. Dorsal view of foetal skull.



Fig. 2. Ventral view of rostrum, foetal.

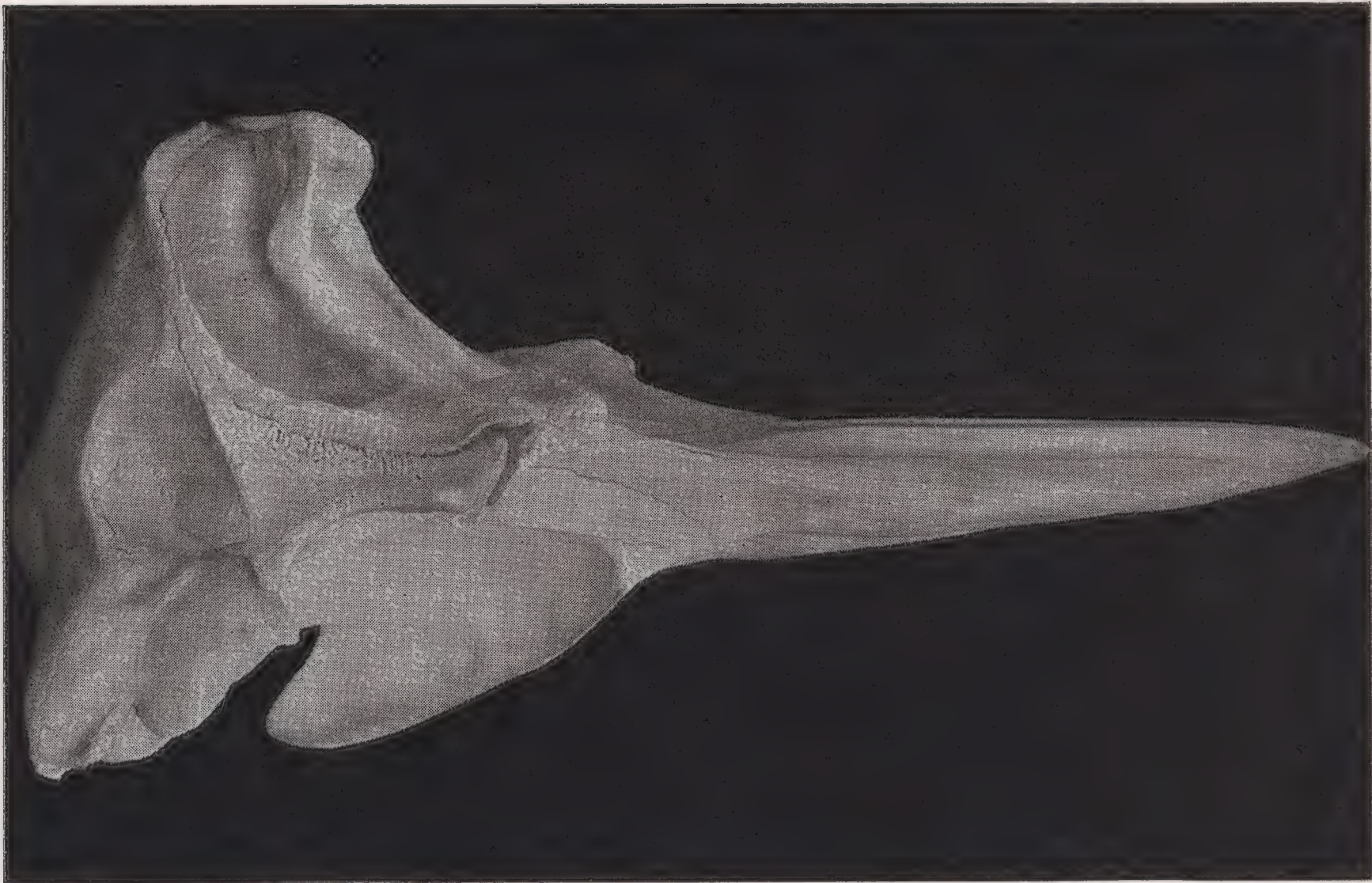


Fig. 1. Lateral view of adult skull.

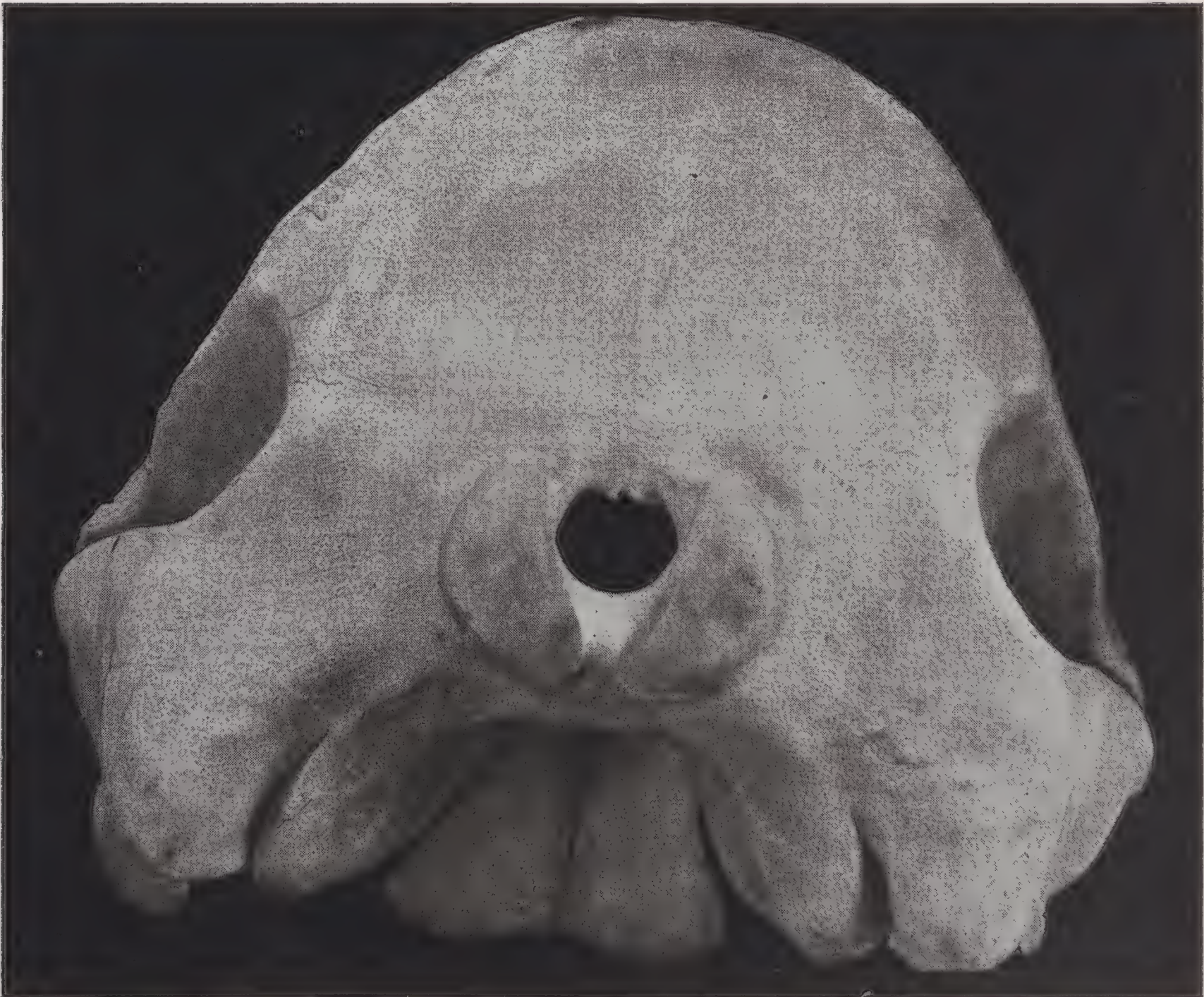


Fig. 2. Caudal view of adult skull.

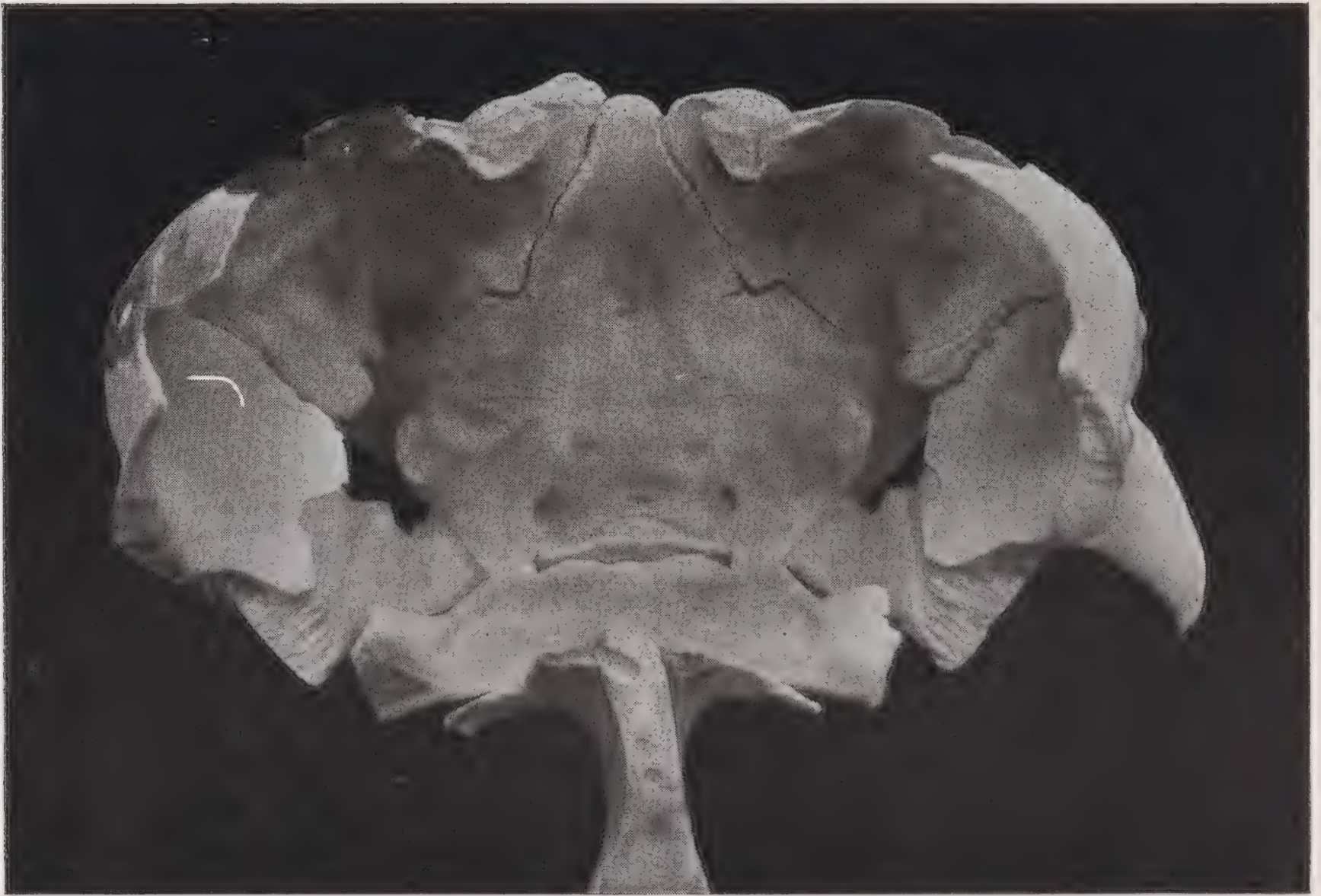


Fig. 1. Floor of cranial cavity, foetal.

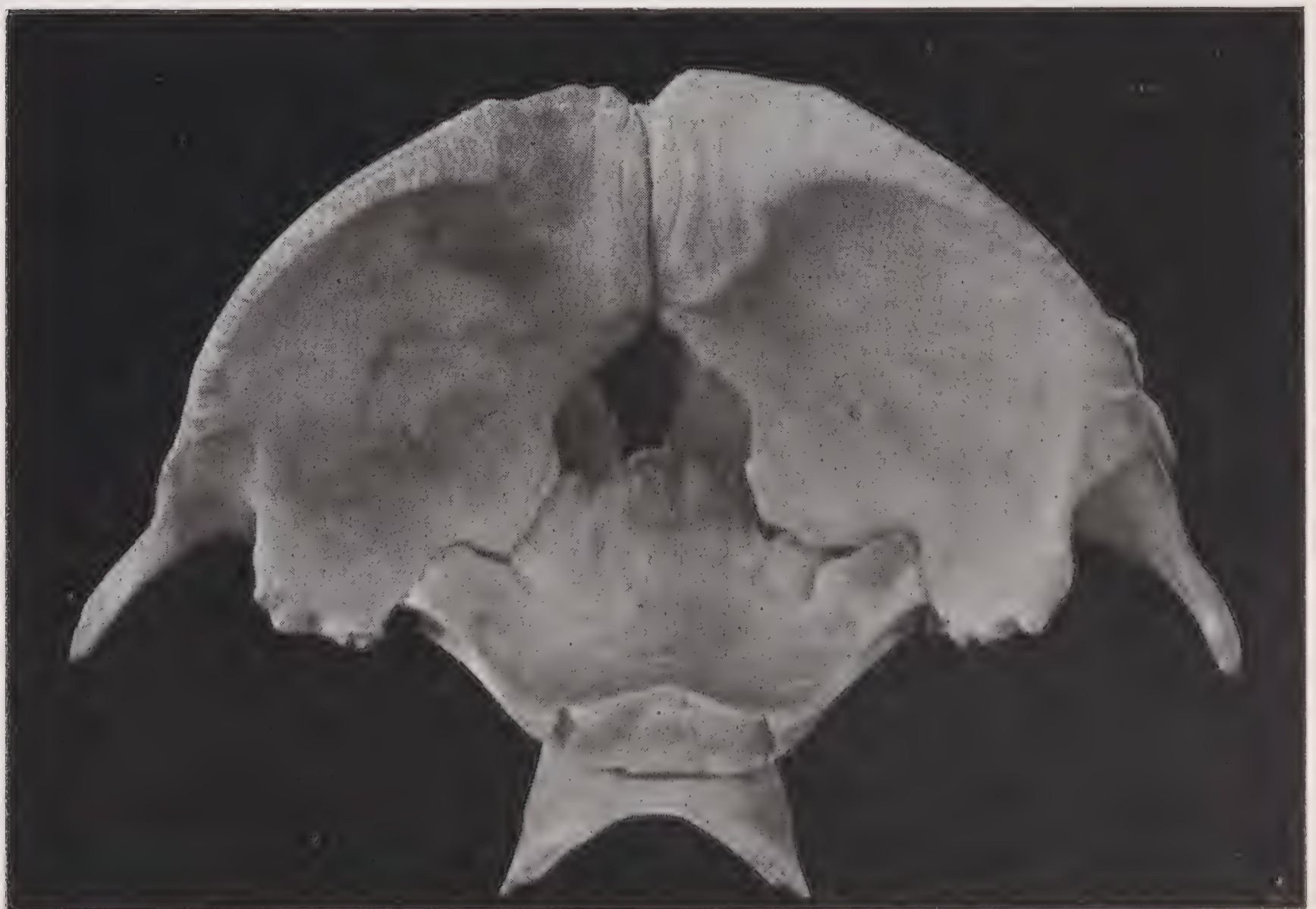


Fig. 2. Rostral wall of cranial cavity, foetal.

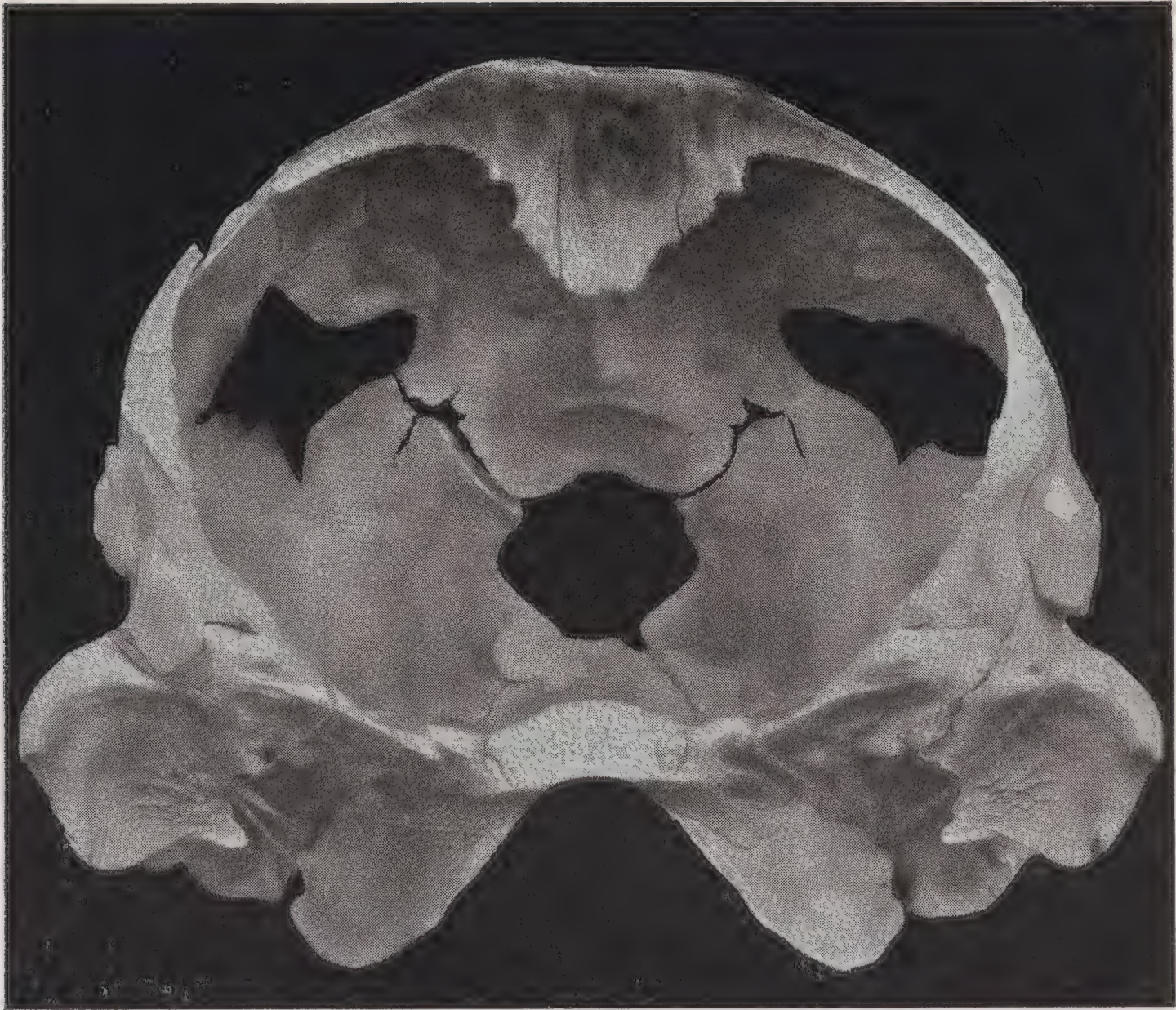


Fig. 1. Caudal wall of cranial cavity, foetal.



Fig. 2. Lateral wall of cranial cavity, foetal.

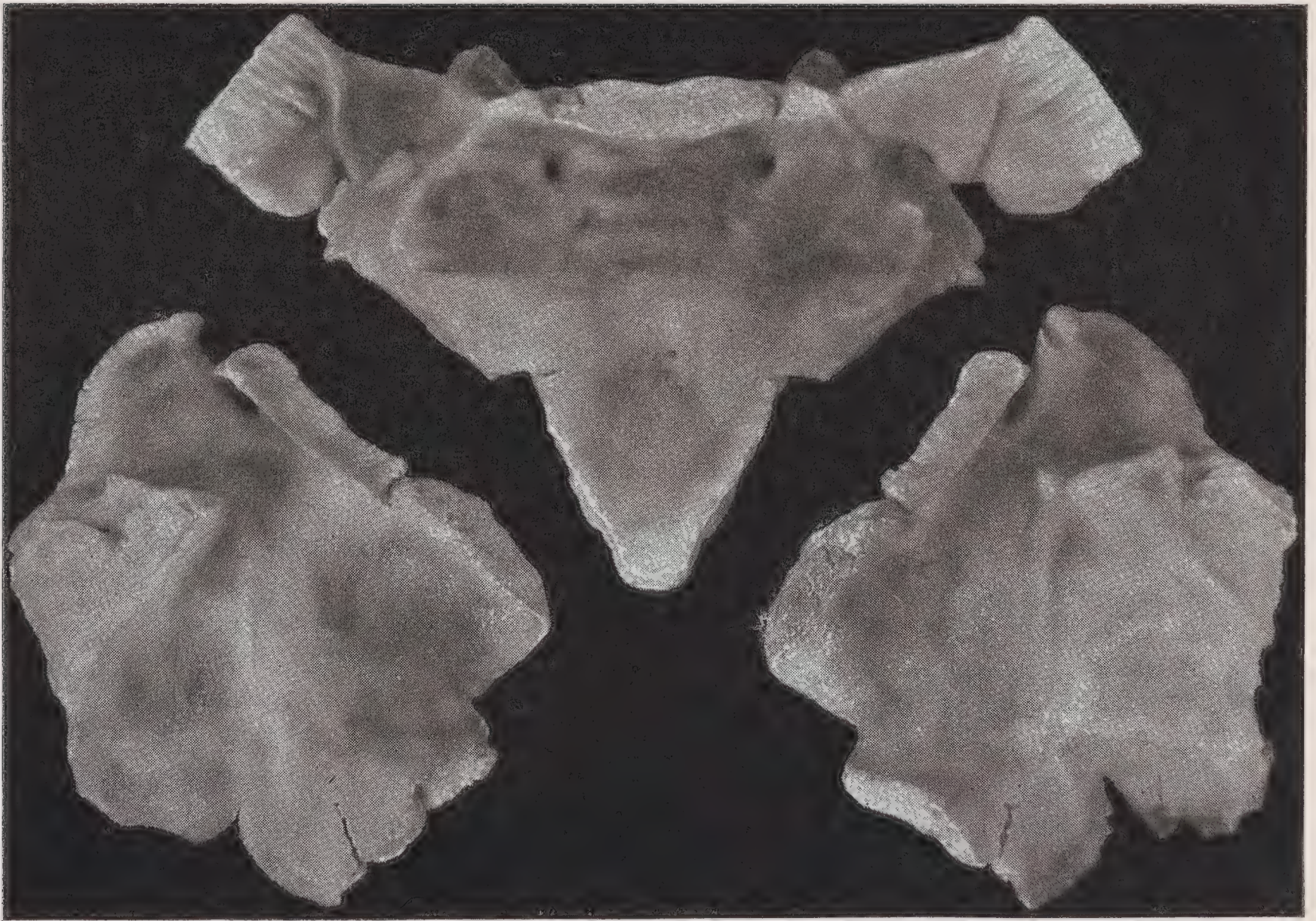


Fig. 1. Basi- and exoccipitals, ental aspect, foetal.

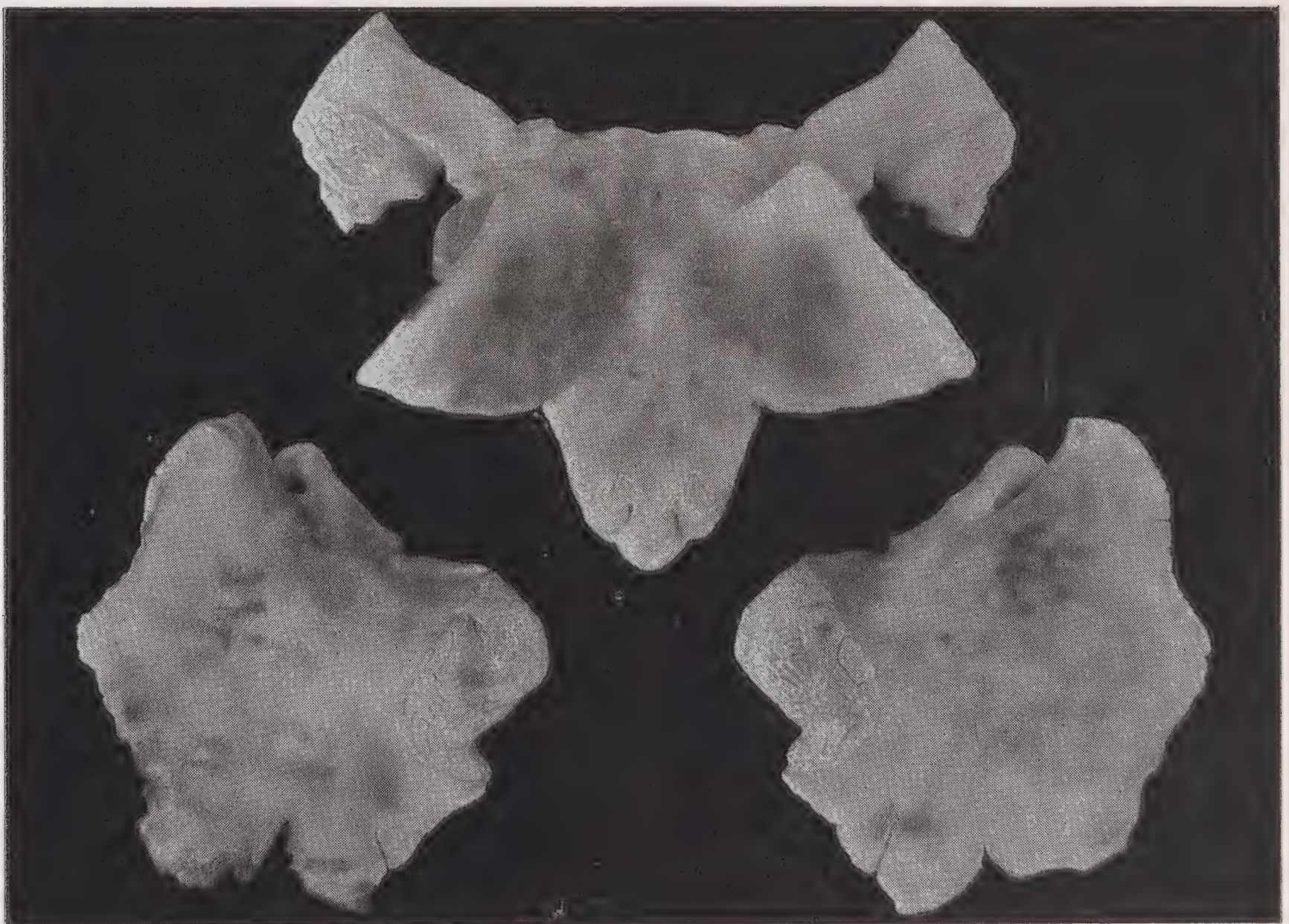


Fig. 2. Basi- and exoccipitals, ectal aspect, foetal.



Fig. 1. Base of skull, otic region, adult.



Fig. 2. Base of skull, otic region, foetal.



Fig. 1. Dorsal view of maxillæ, foetal.

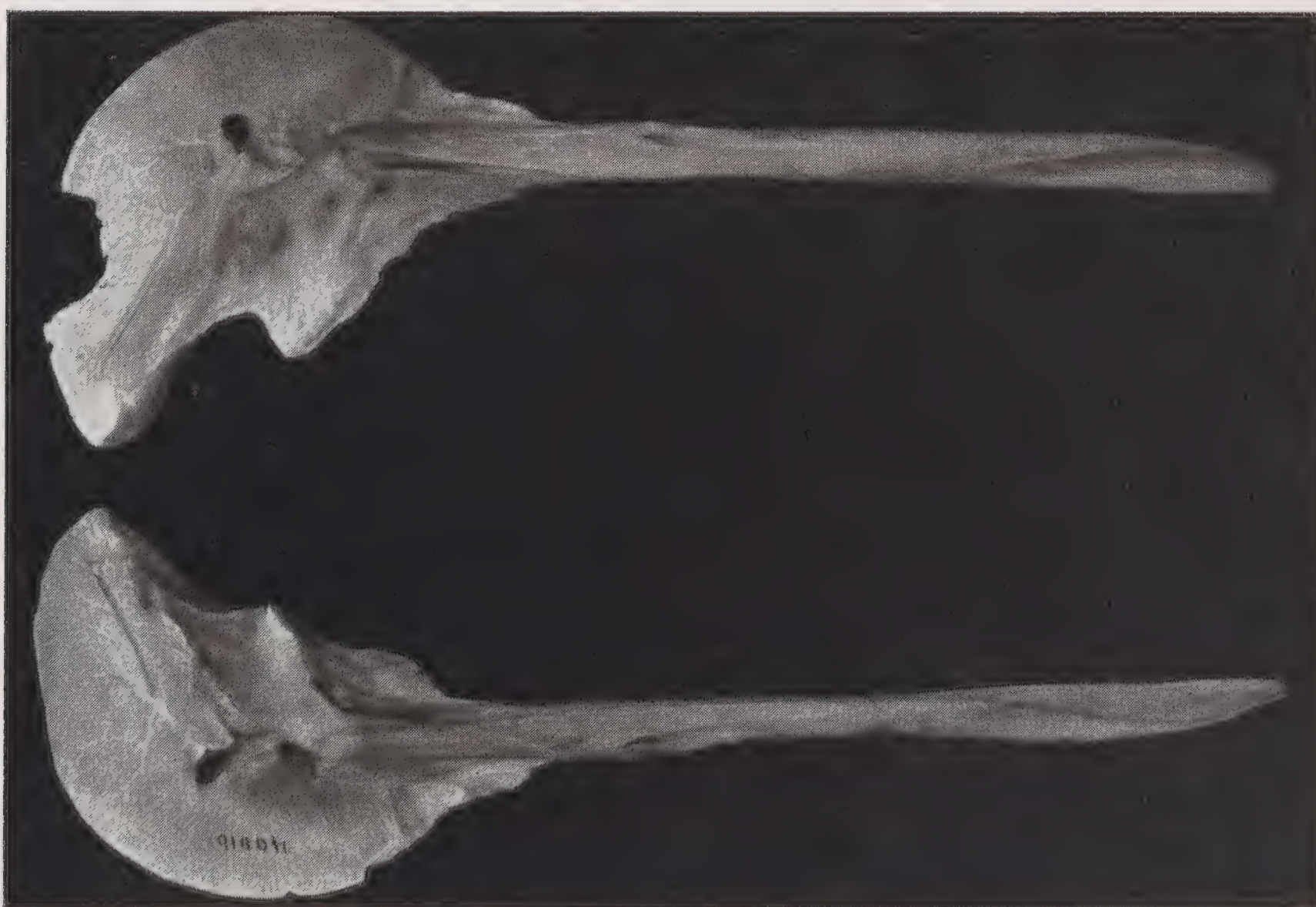


Fig. 2. Ventral view of maxillæ, foetal.

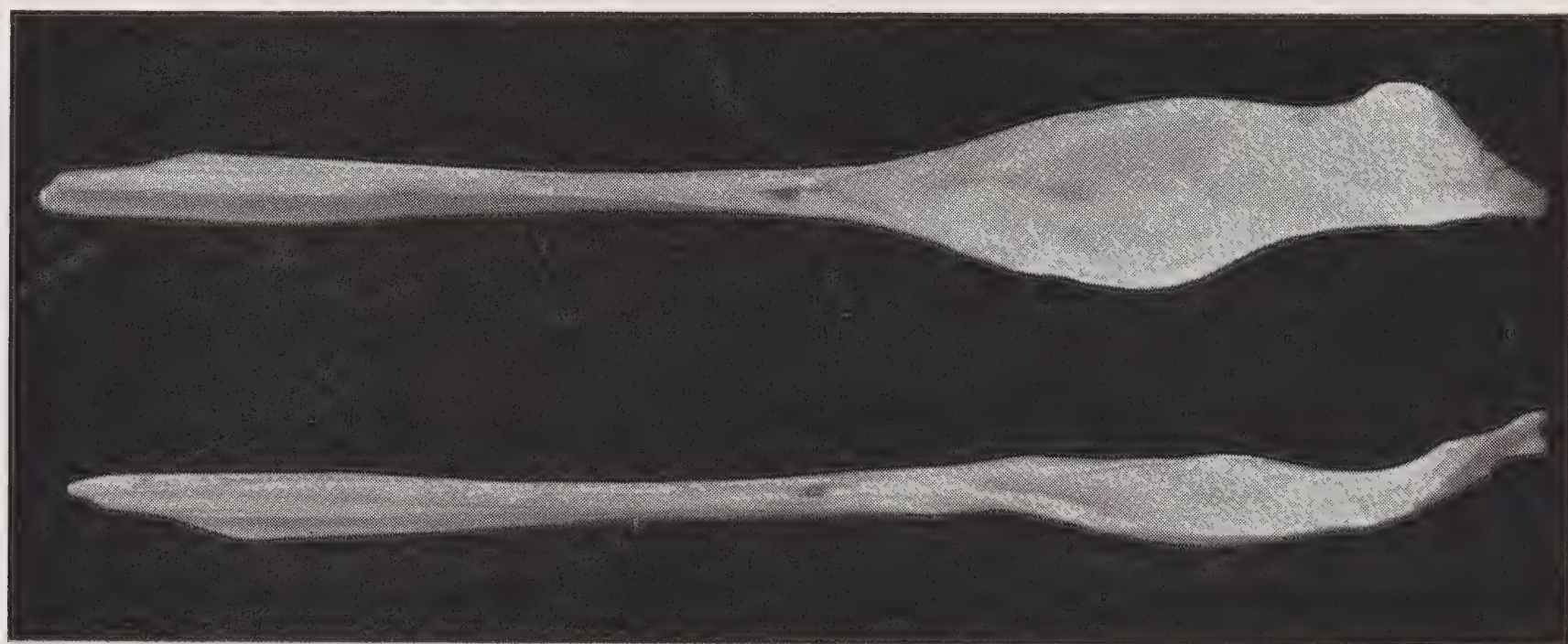


Fig. 1. Dorsal view of premaxillæ.

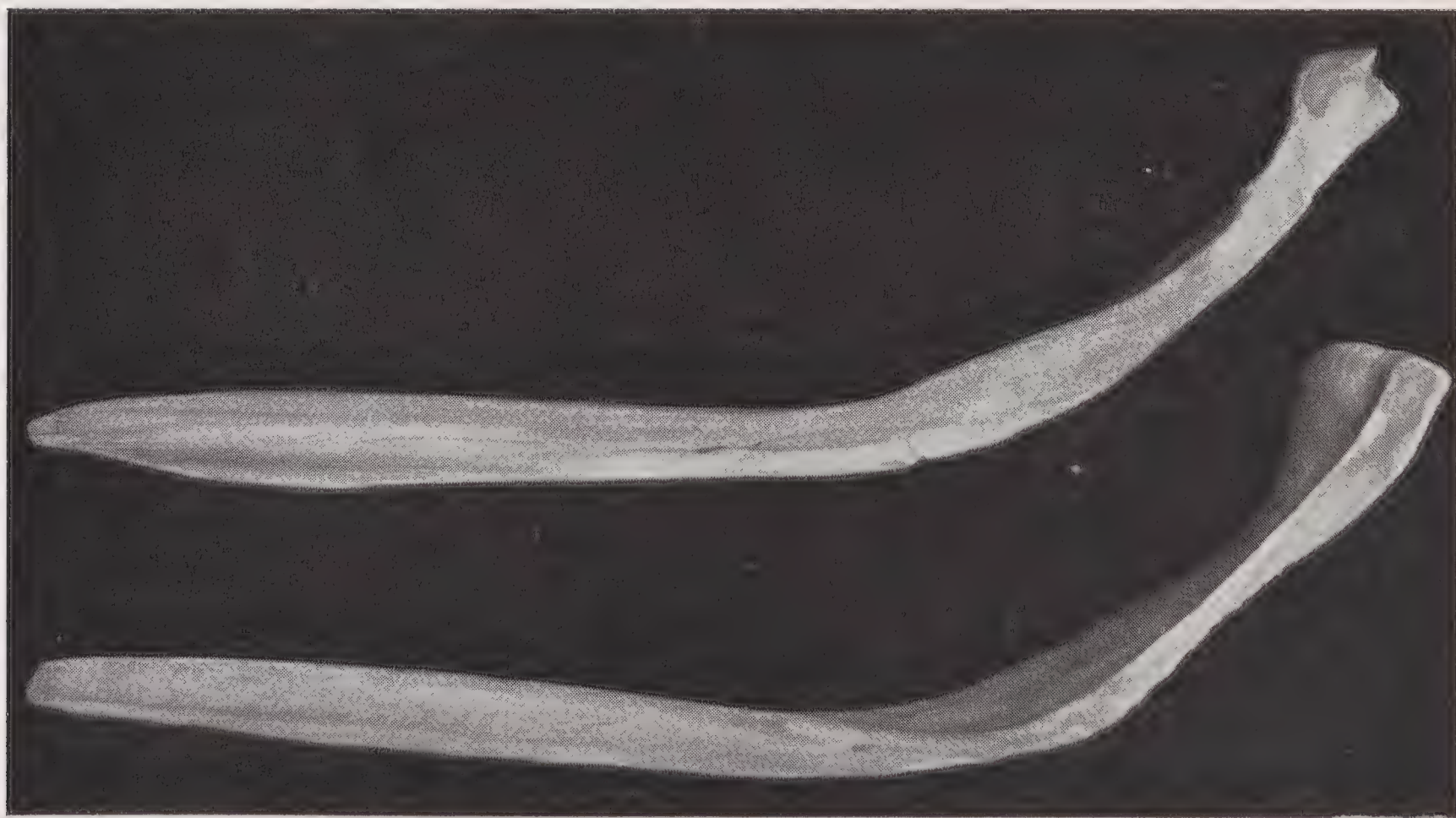


Fig. 2. Lateral aspect, left premaxilla (above), and mesal aspect, right premaxilla (below).

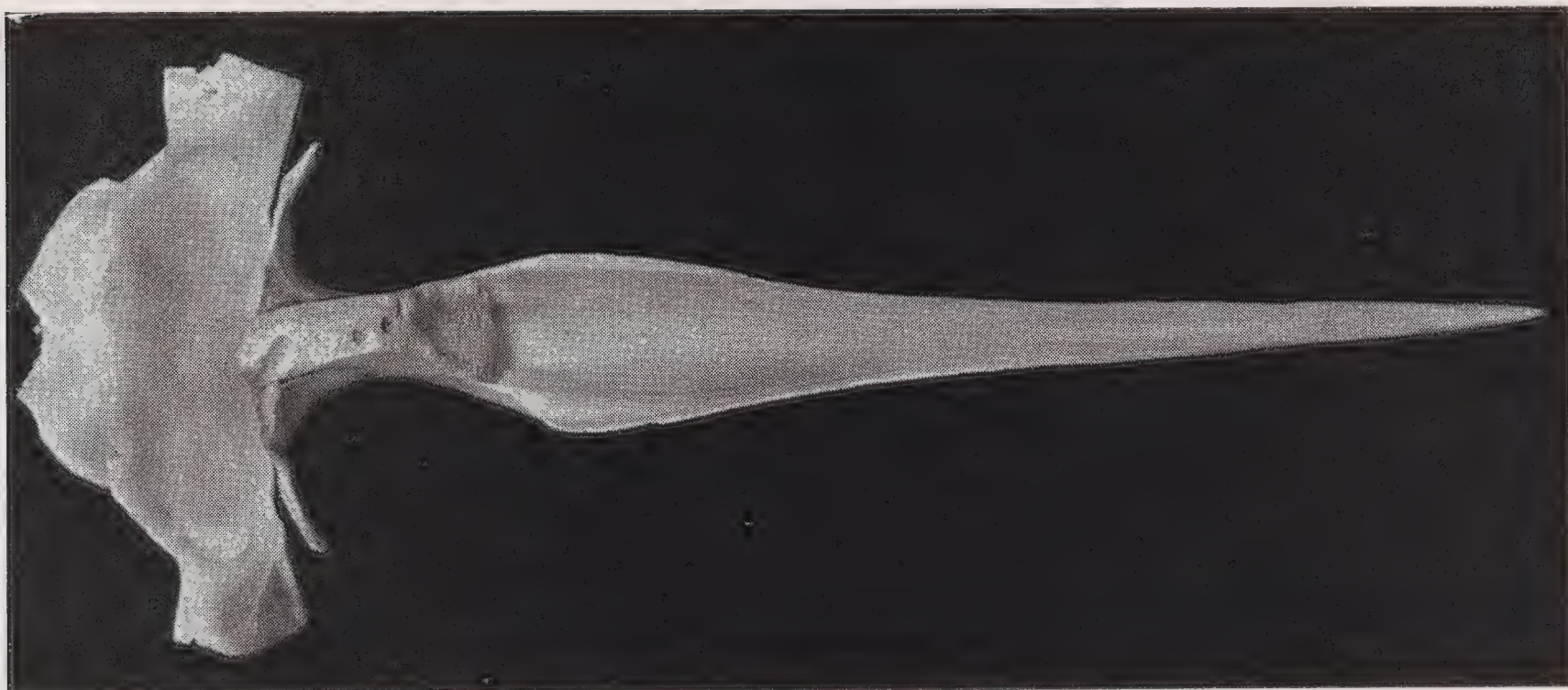


Fig. 1. Dorsum of vomer, mesethmoid, and presphenoid.

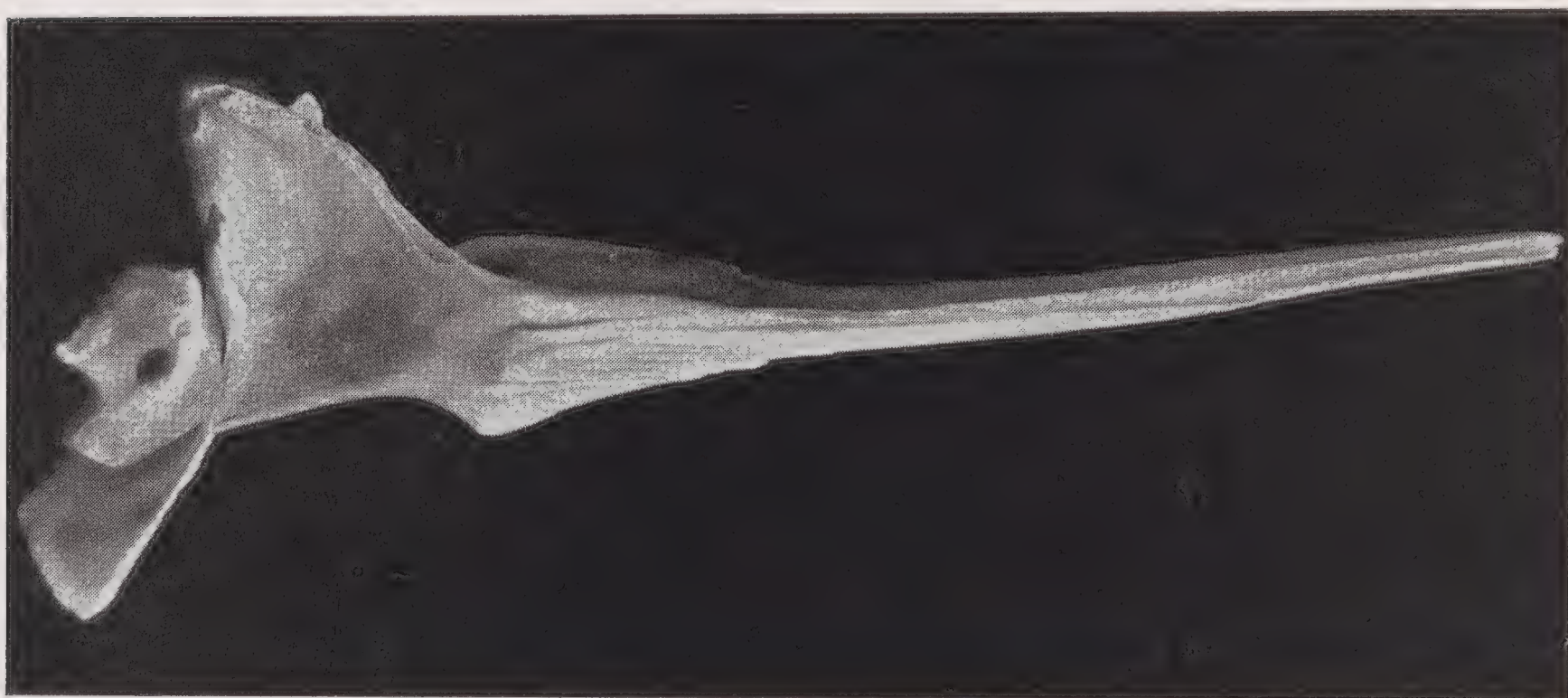


Fig. 2. Lateral aspect of vomer, mesethmoid, and presphenoid.



Fig. 3. Ventral aspect of vomer, mesethmoid, and presphenoid.

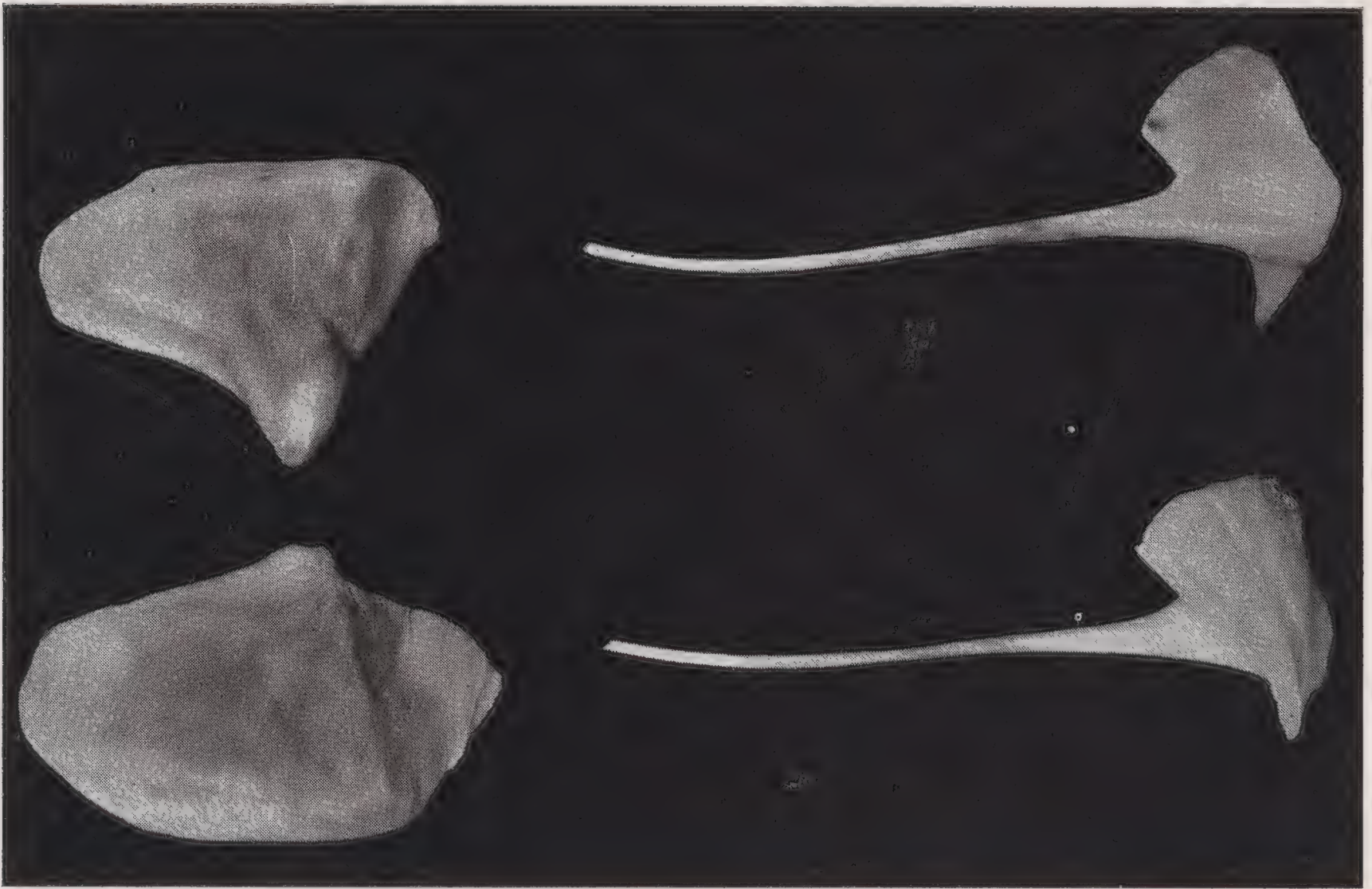


Fig. 1. Nasal and jugal bones.

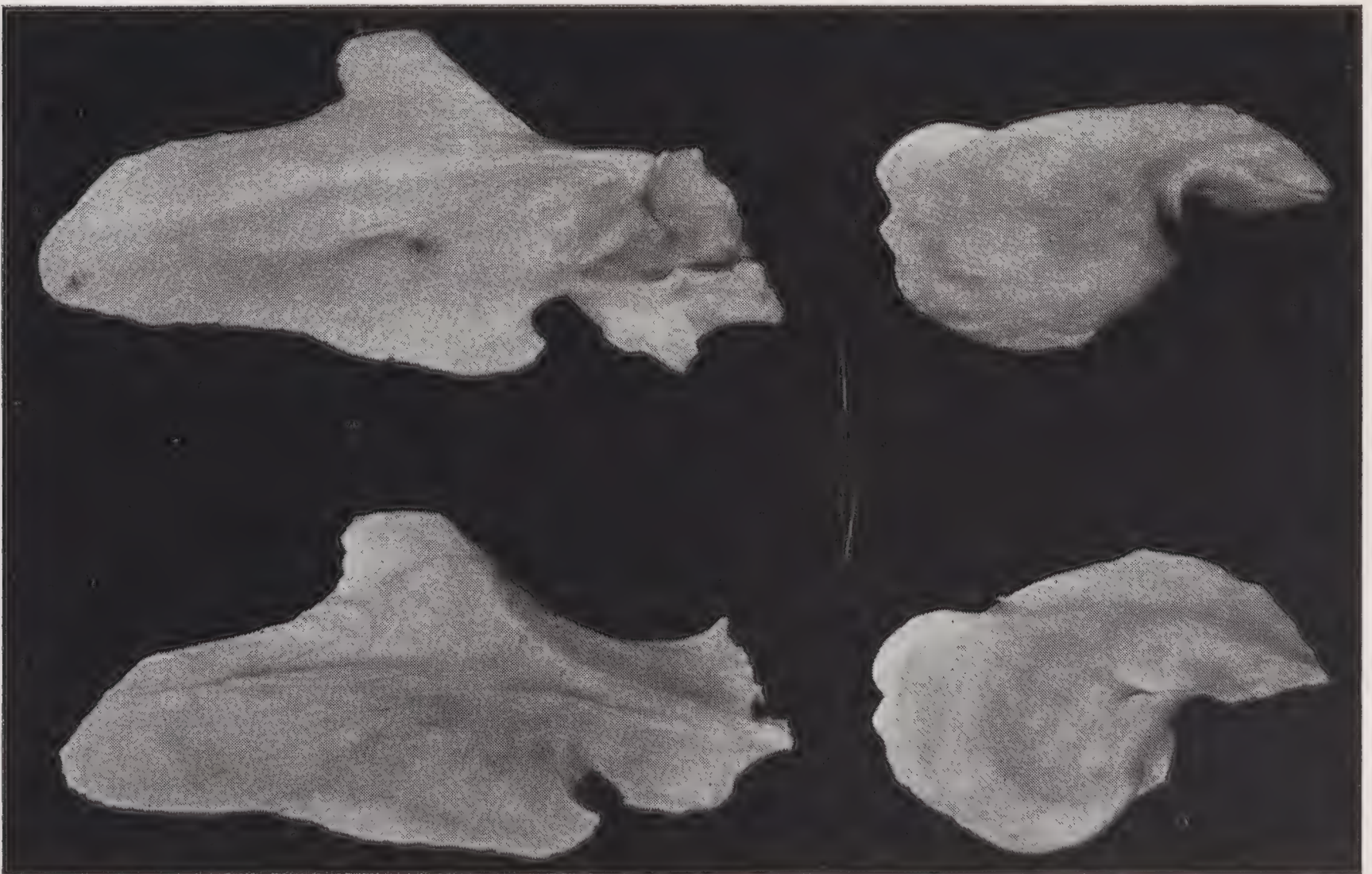


Fig. 2. Palate and lachrymal bones.



Fig. 1. Pterygoids.



Fig. 2. Periotic and tympanic bones.



Fig. 1. Mandible.

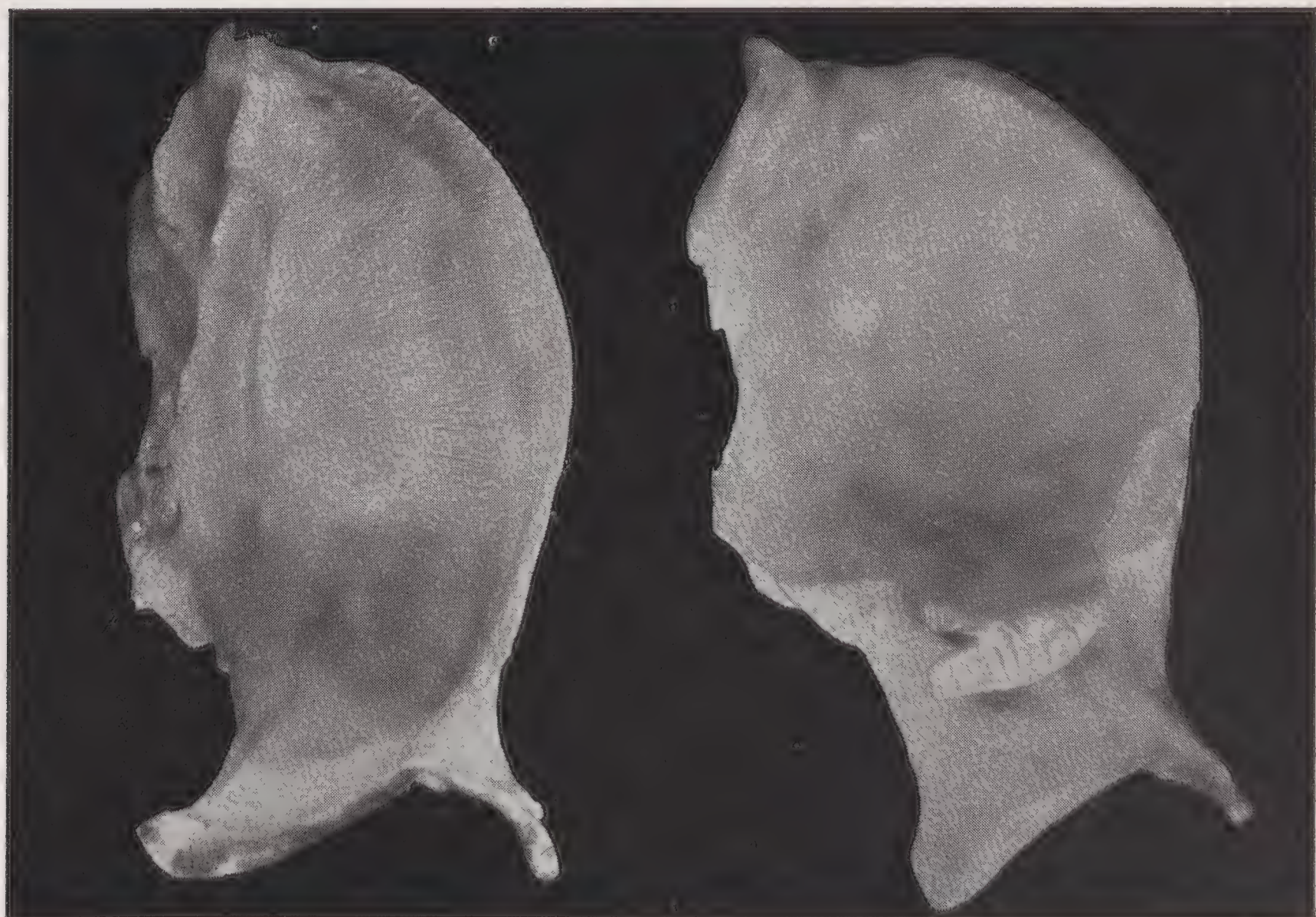


Fig. 2. Frontal.

Article XII.—ON THE ANATOMY OF *OZOBRANCHUS BRANCHIATUS* (MENZIES)

BY W. G. MACCALLUM AND G. A. MACCALLUM

PLATES XXXIII TO XXXVIII

Early in 1915, Mr. Mowbray of the New York Aquarium, while collecting fishes at Key West, Fla., found a lot of leeches on the skin of a large green turtle (*Chelonia mydas*). Most of these were attached under the flippers, where there were also eggs laid in batches upon the skin and covered with a chitinous material which hardens after the deposit of the eggs and holds them in place until they are hatched. A few young worms were found attached to the ventral surface of the adults.

The most striking character of these leeches consists in their having a thick fringe of gill filaments along each side of the anterior part of the body, but it is also to be noted that the anterior sucker is very inconspicuous and that there is no such sharply demarcated neck as is seen in some closely allied forms.

At first it was thought that these must be representatives of the genus *Branchellion*, on account of the presence of definite gills, but a review of the literature of that genus, after a study of the anatomy of this worm, showed that there are very great differences both in external form and in the structure and arrangement of the internal organs. No further consideration of that genus need be given here except in the form of references to the papers of de Quatrefages¹ and Sukatschoff,² where detailed descriptions are given with beautiful plates. De Quatrefages mentioned the fact that Archibald Menzies had found another form of leech provided with gills and parasitic on a turtle in the Pacific Ocean, and, since the name *Hirudo branchiata* given by Menzies did not seem correct, he suggested the generic name *Ozobranchus* (oḡos, branch). The genus is, therefore, referred to de Quatrefages, although he never saw the worm, and Menzies' description³ is quite good. It is so short that it may be quoted in full.

H. depressa attenuata albida, setis lateralibus ramosis utrinque 7, interaneis fuscis bifidis perlucetibus.

Habitat in Oceano Pacifico, testudini adhaerens.

¹ de Quatrefages, 1852, Ann. Sci. Nat. (Zool.), (3), XVIII, p. 283.

² Sukatschoff, 1912, Mitth. Zool. Stat. Neapel, XX, p. 395.

³ A. Menzies, 1791, Trans. Linn. Soc. London, I, p. 188, Pl. xvii.

The body, when moving, is about an inch long, of a whitish pellucid colour, soft, depressed, annulated with fine rugæ, and towards the head attenuated, having a row of soft pellucid branchy bristles on each side, opposite to one another, making in all seven pair. The head is small and truncated; but the other extremity is larger, round, and dilated. The entrails appear through the body, bifid, and of a dark brown colour.

This species was found in great abundance adhering to a turtle, in the Pacific Ocean between the tropics.

I have been able to find no further reference to this genus prior to Oka.¹ He grouped it with the Ichthyobdellidæ making two subgroups, of which one includes *Pontobdella*, *Ichthyobdella*, *Trachelobdella*, *Callobdella* and *Ozobranchus*; the other, *Carcinobdella* and *Piscicola*. He defined the genus *Ozobranchus* as follows, referring it to de Quatrefages, 1852.

Body small, distinct neck and trunk with 5-7 pairs of tufted gills. Skin smooth: anterior sucker small and not distinguished from the neck, segmented on its dorsal aspect. Posterior sucker large hemispherical and distinct. Somites of the neck formed of two equal segments, those of the trunk of two unequal rings. Parasitic on marine turtles.

He described a new species, *O. jantseanus*, found upon a turtle in Wu-Chang, China; it is a form like *O. branchiatus*, which he seems to have studied and described in a previous paper (1895, Zool. Magazine) which is not accessible to us. But, in Vol. V of the *Annotationes Zoologicae*, he discusses the circulation and the body cavity of *O. branchiatus* and decides that the blood vessels form a closed circulation with dorsal and ventral muscular trunks lying above and below the intestine. These blood vessels have no connection with the body cavity; the latter branches throughout the body in capillary form and supplies the branches which carry fluid through the gills. Thus it is the fluid of the body cavity which circulates in the gills and not the blood. A similar idea was expressed by de Quatrefages for *Branchellion* but seems to us open to grave doubt. Oka's description of the genital organs of *O. jantseanus* agrees in general with what we have found in the form we have studied, except that he describes a vagina opening into the posterior surface of the cirrus sac and connected with the ovaries by way of narrow tubes which run through saccular seminal reservoirs. This would be a most anomalous arrangement and it seems from a study of *O. branchiatus* that the supposed vagina is really a sort of seminal vesicle, because it connects not with the ovaries but with the complex enlargements of the vasa deferentia and opens directly into the bulbus ejaculatorius.

¹ Oka, 1902, *Annot. Zool.*, Japan, IV, p. 49; 1904, *idem*, V, p. 133; 1910, *idem*, VII, p. 165; 1912, *idem*, VIII, pp. 1-4. 1895, *Zool. Magazine*, Tokyo, VII, No. 75.

This will be described in detail later. Oka mentions three species as forming the genus *Ozobranchus*: *O. margo* Apathy, with 5 gills; *O. branchiatus* (Menzies), with 7 gills; *O. jantseanus* Oka, with 11 gills. In addition to these, Harding¹ has described a small form parasitic on a terrapin (*Nicoria trijuga*) in Ceylon, which measures 5 mm. in length and has 11 pairs of digitate branchiæ. This he names *Ozobranchus shipleyi*.

The specimens, from which the following study was made, had lain in alcohol a long time, so that the bodies were much contracted and shrunken and no accurate measurements could be made. Furthermore, it was impossible to determine the original color, or to count the segments carefully, or even to make very good sections. It is hoped that at some future time live specimens may be obtained and properly fixed for study, because there are many points in the structure which are extremely interesting but which have been slurred over here or very imperfectly studied because the material was not good enough.

EXTERNAL CHARACTERS

The mature leech (Pl. XXXIII, fig. 1) attains a length of 6 mm., when contracted, with a maximum width of 3 mm., and is of a dirty white color with the contents of the rectum showing through. In the fixed specimens the body arches dorsally and is concave ventrally. There is a short, protrusible neck, which seems capable of being retracted slightly within a ring formed by the first segments of the body. This can be made out very easily in longitudinal sections and is distinguished by the corrugations of its surface which differ somewhat from those of the rest of the body. The mouth is terminal but directed ventrally. It is unarmed. The large posterior sucker is about 2 mm. in diameter. In the mid-ventral line, at about the junction of the two anterior thirds of the body, there are two genital openings, the orifice of male apparatus lying directly in front of that of the uterus. The eyes are no longer visible.

The gills form a compact fringe on each side of the body, arising along the margin throughout the anterior half behind the neck. There are seven trunks on each side, which divide into several filiform prolongations so that there appear to be about thirty-five to forty of the fine threads on each side. They measure 1.5 to 2 mm. in length from their origin at the margin of the body.

It is extremely difficult to count the segmental rings upon the surface

¹ Harding, 1909, Proc. Cambridge Phil. Soc., XV, p. 233.

in the way suggested by C. O. Whitman. There seem to be about forty-five of such rings, counting from the first ring behind the neck to the posterior extremity, but it appears from longitudinal sections that the finer lines correspond with slighter depressions of the surface upon each of the projecting rings. Indeed, these are so irregular that it is frequently impossible to decide what constitutes a whole ring, since the secondary rings are sometimes quite deep. The real difficulty lies, however, in the fact that it is impossible to make out that these superficial rugæ correspond with any segmental divisions of the interior of the body. In sections taken longitudinally in either plane, there are seen to be some transverse septa in the middle of the body which separate such organs as the paired testes, nephridia, etc., so that they evidently lie segmentally arranged, but in the anterior and posterior parts of the body this segmental arrangement is much obscured and not at all easily recognized. At any rate, the true segments must be fewer than the indentations on the surface of the body. The failure to count the segments precisely and to correlate the position of the organs with the numbered segments must constitute a serious weakness in the description of this leech in the eyes of such as Whitman who have made this segmental arrangement such an essential diagnostic factor in the study of leeches.

INTERNAL STRUCTURE

The *digestive tract* (Pl. XXXIII, fig. 2; Pl. XXXIV, figs. 1 and 2, Pl. XXXV) is extremely complicated and well adapted to the accommodation and gradual digestion of a large quantity of blood. The mouth is rounded in outline and furnished with smooth, slightly incurved, thick lips. It is not surrounded by an especially powerful muscle which could act as a sucker nor does it open directly backward into any large tube communicating with the pharynx. Instead, there is a minute orifice on the upper edge of the anterior incurved margin in the middle line from which a very narrow canal curves upward and forward through the substance of the extreme anterior extremity of the head to pass backward over the cavity of the mouth and join the pharynx behind it. The pharynx is a somewhat contorted tube, wider in calibre than this very narrow canal and provided with a very thick muscular wall. Possibly it may act by peristaltic movements as a sucker to draw blood into the digestive tract, and no doubt this is its function. It is partly surrounded by the great nervous ganglion (Pl. XXXVII, fig. 1), partly by a group of enormous cells whose nature we could not determine. They are far larger than any other cells in the body and contain many granules, of which those collected on one side of the cell stain blue in sharp

contrast with the shining eosin-stained granules on the other side. No definite connection by means of duct or protoplasm prolongation between these and the pharynx could be traced. Yet it seemed from their structure that they must have some secretory function and might possibly act as salivary glands.

A narrow thin-walled tube which may be called the oesophagus passes backward from the pharynx. The wall is much plicated (Pl. XXXV) and lined with indefinite, low, deeply staining cells, which seem to present a hyaline margin to the lumen. Almost immediately it receives the ducts of two laterally placed branching glands which are lined with flattened cells which stain very deeply and are provided with rather large nuclei and a ragged cell protoplasm. Again the function of these glands can only be surmised.

The oesophagus broadens laterally and becomes a flattened, arched channel of considerable width which extends back to a point posterior to the middle of the body. It can hardly be called an oesophagus throughout all this extent but, at any rate, names for the various parts of this digestive tract must soon give out if they are only based on analogies with the digestive tracts of vertebrates. At about its middle point it receives the short ducts from two lateral glands. Except in their greater size these glands appear almost exactly like those which join it more anteriorly. Posteriorly, the flattened channel narrows and dips ventrally to a kind of transverse canal, which is very much complicated by the numerous foldings of its walls but which is readily seen to form wide connections to the right and left with enormous lateral sacs or cœca which extend forward only a little way but reach backward to the end of the body. The great cœca are evidently reservoirs for the storing of blood for leisurely digestion. From the central part of the transverse canal there drops ventrally a tortuous channel which soon assumes a more nearly cylindrical form and passes backward in the midline. It, in its turn, receives on its dorsal aspect in rapid succession four pairs of convoluted cœca, which run dorsally forward and back. These are lined with large, prominent, deeply staining cells (Pl. XXXIV, fig. 2) and are not found to contain any of the yellow material which fills the rest of the digestive tract. In all probability they act as digestive glands. Continuing backward in the median line and passing somewhat dorsalward, the intestinal tract dilates into a fusiform widening, which, after narrowing, extends into a cœcum. Just in front of this cœcum a channel passes ventrally to join the rectum, which, while it projects forward into another cœcum, runs backward and upward to open on the dorsal surface just above the large terminal sucker. Thus the digestive tract falls into a number of parts, which, for the sake of clarity, may be designated prepharynx, pharynx,

oesophagus, oesophageal glands, lateral reservoirs, intestine, intestinal cœca, and rectum.

The *circulatory system* (Pl. XXXIV, fig. 1; Plate XXXV) is composed chiefly of great sinuses, which have a rough segmental arrangement and are lined by an endothelium which is peculiar in that the cells appear to be rather loosely arranged and loosely attached. They are quite voluminous and are often seen to project into the cavity of the sinus or to hang partly free in its lumen, being attached to the wall for part only of their length. The sinuses are separated in the middle of the body, at least, by septa made up of various tissues. The organs hang suspended in them in many places so as to come into very intimate contact with the blood.

It is obvious that there must be a propulsive power to keep the blood in motion but, while some evidences of this were found, all our efforts have failed to reconstruct the arterial system clearly and this is one of several features which we must leave incompletely described.

In one series of sections there is visible among the lobules of the female generative organs a muscular tissue which on each side of the median line becomes concentrated at different anteroposterior levels into sac-like structures, the cavity of which is in each case full of blood and in open communication with the cavity of the large central venous sinuses. These are not to be found in other series and we are in doubt as to their interpretation. At first it seemed possible that they might represent a sort of heart but this is hardly probable since the musculature, if such it be, extends quite round the lobules of the yolk gland in such a way as to be useless, in that situation at least, in the propulsion of blood.

Above the oesophagus an arterial tube can be traced in the middle line for some distance forward and backward, but there is no apparent connection with the heart-like mass or with other canals. Laterally there are two wide, thin-walled tubes conveying blood; these are cylindrical in form and continue through most of the length of the worm. They are probably arteries and, although their walls are thin, they may be contractile. They give off branches to the gills, from which the blood is returned by two venous channels which empty into the large, lateral, venous sinuses.

It is quite clear that the statement made by de Quatrefages about the non-existence of blood in the channels of the gills is an error, because blood is plainly seen there. He claimed to have injected the blood vessels with a colored mass which did not enter the gills, for which reason he thought that the vessels of the gills contained only lymph.

The blood is a rather refractive fluid which stains pink with eosin and is moderately rich in nucleated cells which do not stain especially deeply. The fixation is such that little can be made out of the blood cells but they

seem to be of one type, elongated or elliptical, not noticeably granular, and provided with a single rounded or irregular nucleus. They are much smaller than the endothelial cells and measure about $5\ \mu$ in diameter.

The Male Genital Apparatus

The worm is, of course, hermaphroditic and the male genital apparatus is so complicated that it is drawn separately in plate XXXVI, figure 1. There are four pairs of testes, from which narrow ducts lead to two convoluted masses of thick walled tubes which, in turn, send twisted canals to the median ejaculatory bulb. But the latter also send from each side a narrow tube which, uniting with its fellow in the midline, empties into a reservoir which is connected by a wide muscular channel with the cavity of the *bulbus ejaculatorius*.

The testes are elliptical in form and lie in successive segments a little in front of the middle of the body and far toward the lateral margin. Their long axes run dorsoventrally. From the posterior surface of each testis there springs a thin-walled narrow vas efferens which curves round the ventral end and runs upon the anterior wall. Thence it passes forward to the posterior aspect of the next anterior segmental septum, pierces it, and curves outward to return and join a similar vas efferens from the next testis. At first it seemed that all the vasa efferentia pursued their whole course to the seminal vesicles independently but more careful study showed that they really unite, above the sinuses in which the testes hang, into a long vas deferens on each side which then runs forward piercing successive septa to a point three segments in front of the anterior testis, where it turns inward and downward toward the middle line and passes somewhat backward once more to lose itself in the seminal vesicle. The vas deferens can be traced into this convoluted mass, where the character of its wall changes. The tubules of the seminal vesicles (Pl. XXXV) are thick-walled, muscular, and filled with spermatozoa. They are surrounded by a layer of blue-staining cells. The seminal vesicle on each side presents two diverticula of different types and gives off two canals. Of the diverticula, one is a round sac connected by a short narrow neck with the convoluted canal. It is covered, like the rest, with blue-staining cells, has a rather thick pink-staining wall, and is full of spermatozoa. The other is smaller and elongated and also connected with the muscular common canal. It is not covered with a mantle of cells, is thin-walled, without evident structure, and is quite empty or else contains perfectly clear fluid.

Of the two canals given off from the seminal vesicles, one passes forward

with many convolutions to enter the ejaculatory bulb at its base and to open into one of the branches of its cavity. The other passes toward the midline ventrally and meets its fellow of the opposite side to form a channel which runs ventrally still to enter a large rounded sac with epithelial lining and bluish granular contents. This sac sends a wide thick-walled channel forward to empty directly into the cavity of the ejaculatory bulb. It is like a diverticulum of the bulb with folded walls of the same appearance as those which line the bulb itself. It is quite clear that this is what Oka describes as a vagina with delicate canals connecting it with a transverse bridge of ovarian tissue which joins the two ovaries. He thinks that the uterus does not serve as a channel for fertilization but that this canal, opening, as he describes it, into the cirrus sac into which the penis projects, receives the penis in copulation and thus acts as a vagina. The following out of the connections in serial sections is pretty clear with regard to this particular structure however and there is no doubt that the connections are actually with the seminal vesicles. It must, therefore, constitute a sort of seminal reservoir, emptying the spermatozoa which overflow from the tubular seminal vesicles into the ejaculatory bulb at the time of ejaculation. The ejaculatory bulb itself projects a short way into the wider canal, which opens externally. It is quite muscular and evidently protrusible.

The Female Genitalia

The female genitalia (Pl. XXXVI, fig. 2; cf. also Pl. XXXIV, fig. 1) consist essentially of paired ovaries with associated yolk glands, which open through two wide ducts into the straight tubular uterus whose external orifice lies in the median line just behind the *bulbus ejaculatorius*. The ovaries with their yolk glands lie at about the middle of the body or a little anterior to this and are found on each side of the midline. The lobulated yolk gland extends laterally and backward, the ovary proper riding on its dorsal, anterior, and mesial surfaces. This description is vague because it is really difficult to determine the relation of the ovary to the yolk gland more precisely, inasmuch as they are so intimately united and lobules of the ovary are found interlaced with convolutions of the yolk gland. The more distal parts of the yolk gland have a somewhat saccular character, while the proximal parts are composed of anastomosing thin-walled sacs of large size filled with hyaline globules. The distal parts are different in that their walls are made up of large, indistinctly outlined cells, which have a bluish-staining protoplasm in which there are many pink-staining droplets of all sizes. These evidently exude into the sac and coalesce to form the highly refractive

pink-staining globules which fill the larger sacs. They look much like red blood corpuscles but are less uniform in size and shape. Apparently, they must be regarded as the yolk which goes to the formation of the eggs, although the direct application of this to the ova is not to be seen in these specimens. The thin-walled sacs are in such wide communication that they form practically one, broad, coiled or folded tube.

The ovary is even more indistinct in the outline of its convolutions, although it is, as a whole, sharply outlined by the surrounding capsule which covers it and extends to the yolk gland. It is composed of numerous folds or layers of cells, which appear to begin as small ova with relatively large nucleus and to grow, as one proceeds to follow along the convolutions of the layer of cells, until they become very large, finely granular cells with relatively abundant protoplasm. In places, and especially as the column of cells approaches the oviduct, there appear what must be ripe ova — huge masses of densely blue-staining protoplasm, each with a pale vesicular nucleus and distinct nucleolus. The protoplasm is finely granular but the granules are so fine as to give a ground-glass appearance.

It is difficult to determine the course of the products of the genital glands toward the uterus since there are only two channels which, running each from one side, join to form the uterine tube. The sacculated tube of the yolk gland is, in most of the sections, completely bounded by its own walls but in places the separation between the cells of the ovary and the refractive yolk globules becomes almost indistinguishable. Nevertheless, there are no yolk globules found among the loosely arranged ova. In cross-sections, it is plainly seen that the oviducts open from the anterior end of the ovarian portion of the mass and proceed directly to join to form the uterus. In that case, the riper ova are nearest the oviduct, although some other large ova are scattered elsewhere, and it is necessary to suppose that the yolk must filter through among the folds of the ovary to surround the ripe ova and enter the oviduct. In a longitudinal series, this is the case on one side but on the other it is a portion of the sac which has the character of a yolk organ which opens directly into the oviduct so that, in that case, the ovum must pass through a mass of yolk to reach the oviduct. The impression remains that there is but one sacculated organ on each side, part of which is modified to the production of ova, while another part produces yolk, and that the escape of both is by way of the broad canal which opens anteriorly but that usually the ovarian portion is in most immediate connection with this canal.

There is no obvious shell gland or anything corresponding to a receptaculum seminis. The uterine tube contains no eggs, in any of the specimens examined, and has collapsed into a straight tube with plicated walls, surrounded by relatively thick musculature. The orifice is unarmed.

The Excretory System

Throughout the mid-portion of the body and extending back into the posterior segments, there are paired nephridia, about twelve in number. These are situated in the segmental septa laterally, but ramify dorsally and toward the median line and even over the blood sinuses dorsally to meet those of the adjacent segments. They run ventrally and turn outward through the ventral muscles to open by minute orifices on the ventral surface of the body along a line about one-fifth of the distance from the margin of the body toward the midline. The tubules which make up these organs are about alike in appearance throughout their course and are lined by pink-staining cells in which the protoplasm has something of a palisade arrangement. The lumen is very narrow and is bent at very sharp angles. The cells have very large nuclei with nucleoli, which are, however, not seen in all the cells but seem to be far apart. The coil of tubules is crushed and flattened together in the septum so that it becomes very inconspicuous. The terminations of the tubule could not be found with certainty and no flame cells or funnels were made out with any clearness. Neither could it be determined whether the extremity of the tubule had any closer relation to the blood channel than the remainder nor whether this extremity was in any way connected with the large gland-like parenchyma cells. Probably it merely ends free in a crevice of the body.

The Nervous System

There is a median, ventral, gangliated chain which runs from the region of the posterior sucker forward to a point just behind the genital pore, where it ascends, curving over the bulbus ejaculatorius to reach and encircle the muscular pharynx, spreading out there to form a large ganglionic mass (Pl. XXXVII, fig. 1), which is rather more bulky below than above the pharynx. At the base of the large posterior sucker there is a wide and thick ganglionic plate, from which nerves pass to the musculature of the sucker. The nerve cells with large pale vesicular nuclei closely grouped together assume a marginal position. They are gathered into fairly definite concentrations to form the ganglia of the cord but these concentrations are not very sharply outlined and it becomes difficult, on account of the scattered ganglion cells in the intervals, to count the ganglia. There is one for each segment, however, and about ten are to be found in the abdominal portion of the worm. There are a few thick branches from the cord passing up into

the region of the rectum and maintaining their ganglionic character there, but in front of that the ganglia assume a more segmental character and send off nerves to the musculature (Pl. XXXVII, fig. 2). Within the ganglion the fibres which form these nerves may be seen to decussate, the ganglion cells being arranged at the extreme lateral poles of the ganglion, so that the fibres for those on the right cross those from the left in the midline in passing to the muscles of the opposite side.

After the chain rises to reach the œsophagus it is difficult to distinguish the nerves that pass out to the muscles and other organs.

The eyes, which are perfectly visible in the young and undeveloped leech, are still to be found in the adult but only in sections, since they have sunken into the interior of the anterior part of the body and lie embedded in the parenchyma at some distance below the skin. Only two are to be found and they are spherical, composed of few, peculiar, large, clear cells (Pl. XXXVIII, fig. 1), and partly surrounded by a deeply pigmented layer within which a few nuclei can be discerned. Most careful search failed to reveal any optic nerve passing to these organs and it may be surmised that this has atrophied through disuse.

The fate of these eyes seems very extraordinary and we were tempted at first to think that it was an error to suppose that they were really withdrawn from the surface but, as sections in all directions show the same result, there is no doubt as to their position.

Musculature

The body of the worm is provided with strong muscular layers, and special arrangements are found about the mouth and the posterior sucker. There is an outer layer of circular muscle fibres throughout the trunk and, inside these, longitudinal layers which are somewhat oblique. Some of these fibres spread out in a fan shape into the body of the sucker, which is also provided with vertical fibres running from convex to concave surface and circular fibres which are placed in the margin.

About the mouth there is a much feebler arrangement of small muscle fibres, which run in several directions.

Parenchyma

The general parenchyma of the body is made up of several types of cells, among which two sorts are especially conspicuous. The first of these types consists of enormous cells of all shapes, with rather large vesicular nuclei

and with a very great amount of protoplasm, the granules of which stain deep blue. In addition to these blue granules, which hang together in a coarse network and remind one of the tigroid bodies of nerve cells, the whole central part of the cell about the nucleus and stretching out to one margin is filled with highly refractive pink-staining granules. The nucleus commonly contains several nucleoli which are oval or elliptical. The cells look like the active cells of some gland, but it has not been possible to ascribe any special secretory function to them. They are especially striking through their very great size and the contrast in their staining properties. The second type is found scattered everywhere, but especially among the fibres of the body musculature. These cells are smaller and have small indistinct nuclei. Their protoplasm is filled with fine, bright yellow granules which give the impression of having a lipoid character, although they are not dissolved by alcohol and ether.

In the head region and in the large sucker, there are great numbers of cells which resemble the large type excepting in their smaller size and in the absence of the red granules.

At one point on the back of the neck, just in front of the collar-like ring, there is a peculiar condition. A fold of skin projects and is quite devoid of the usual deeply staining cells which underly the skin. Instead, there is a sweeping bundle of fine channels filled with the red-staining granules, such as are seen in the larger parenchymal cells. No cells are concerned but they seem to be granules set free somewhere deeper in the tissue and stretching along in strands toward this place on the back of the head. The strands pass quite to the skin and appear to penetrate it and to open on the surface as though for the purpose of discharging the granules by many fine outlets. The reason for this and the nature of the whole thing is quite obscure.

The Skin

The skin is very thin over the whole body and quite unarmed. It consists of a thin homogeneous epidermis, under which there is a layer of small cells discontinuously arranged, giving it the appearance of having a fine papillary arrangement. These cells are closely applied to the epidermis. Just beneath the skin, there are many of the larger parenchymal cells but none seem to have the relation of gland cells attached to the skin.

There are, undoubtedly, many tactile sense organs distributed over the skin, but those about the anterior extremity of the head become quite conspicuous and are rather numerous (Pl. XXXVII, figs. 3 and 4). They appear as bud-like projections, bulging through the ordinary skin and termi-

nating externally just in the level of the protruded skin in a bunch of hair-like processes. Below, these fade into a concentrically arranged group of elongated, fusiform cells. Below these, there are two or three very large, pale cells with large central vacuoles which seem to be lined with cilia, although that may be merely the irregularity of the protoplasm. These are quite like the large pale cells of the eye. Although the fine nerve connections which must reach them can not be made out, this seems to be only the effect of the poor fixation of the tissue.

On the inner side of the anterior lip, there are masses of fusiform cells, similarly arranged, so as to converge upon one or two points of the surface, where they apparently act as sensory organs.

The young worms (Pl. XXXVIII, fig. 3) when hatched are only about 1.20 mm. long by .40 wide at the base, where they are widest. The head is narrow; the mouth is well developed but with no sign of a proboscis. They have, on the dorsal lip, two eyes, well shown even at this period. The worm has seven short branchiæ on each side, nearer the back than the abdomen. They are mere stubs but, as they grow, divide and subdivide. The alimentary canal at this stage is only a crooked tube, double at its posterior half and well filled, but no open anus can be seen, although the situation of the prospective opening is apparent at the end of the body dorsal to the sucker. The sucker is large and well developed, and it is probably used at once.

The eggs, found in clusters, measure .8 mm. in diameter and have a double contoured shell (Pl. XXXVIII, fig. 2).

EXPLANATION OF PLATES

PLATE XXXIII

Figure 1. *Ozobranchus branchiatus*. Ventral surface.

Figure 2. *O. branchiatus*. Digestive tract. *Pph.*, prepharynx; *Ph.*, pharynx; *Oes.*, œsophagus; *Oes. g.*, œsophagæ glands; *Int.*, intestine; *Int. c.*, intestinal cœca; *Lat. res.*, lateral reservoirs; *Rect.*, rectum.

PLATE XXXIV

Figure 1. *O. branchiatus*. Horizontal section. *C.*, sinus filled with blood-like fluid; *Gg.*, seven groups of gill filaments; *T.*, testes; *Y. gl.*, yolk gland; *S. v.*, seminal vesicles; other letters as above.

Figure 2. *O. branchiatus*. Cross-section of one of the intestinal cœca. Cf. Pl. XXXIII, fig. 2.

PLATE XXXV

O. branchiatus. Transverse section at level of the ovaries. Letters as before; *Ov.*, ovaries; *C. ns.*, ventral gangliated nerve cord; *S. r.*, seminal reservoir.

PLATE XXXVI

Figure 1. *O. branchiatus*. Male genital apparatus. *T.*, testes; *V. e.*, vasa efferentia; *V. d.*, vas deferens; *S. v.*, seminal vesicles; *D. D.*, diverticula; *S. r.*, seminal reservoir receiving canals from seminal vesicles; *E. b.*, ejaculatory bulb.

Figure 2. *O. branchiatus*. Female genital apparatus. *Ov.*, ovary; *Y. gl.*, yolk gland; *Ut.*, uterus.

PLATE XXXVII

Figure 1. *O. branchiatus*. Muscular pharynx (*Ph.*) surrounded by large ganglionic masses (*C. ns.*) and also by very large gland-like cells (*Gl.*). Numerous parenchyma cells with muscle fibres interspersed surround this area and show the relative sizes of the cells.

Figure 2. *O. branchiatus*. Ganglion of ventral gangliated cord with nerve running to muscle. There is a decussation of the fibres.

Figures 3 and 4. Tactile sense organs on skin of head.

PLATE XXXVIII

Figure 1. *O. branchiatus*. Submerged eye lying deep in the parenchyma and muscle.

Figure 2. *O. branchiatus*. Eggs from skin of the host.

Figure 3. *O. branchiatus*. Young worm showing eyes, rudimentary gills, and undeveloped intestinal tract.

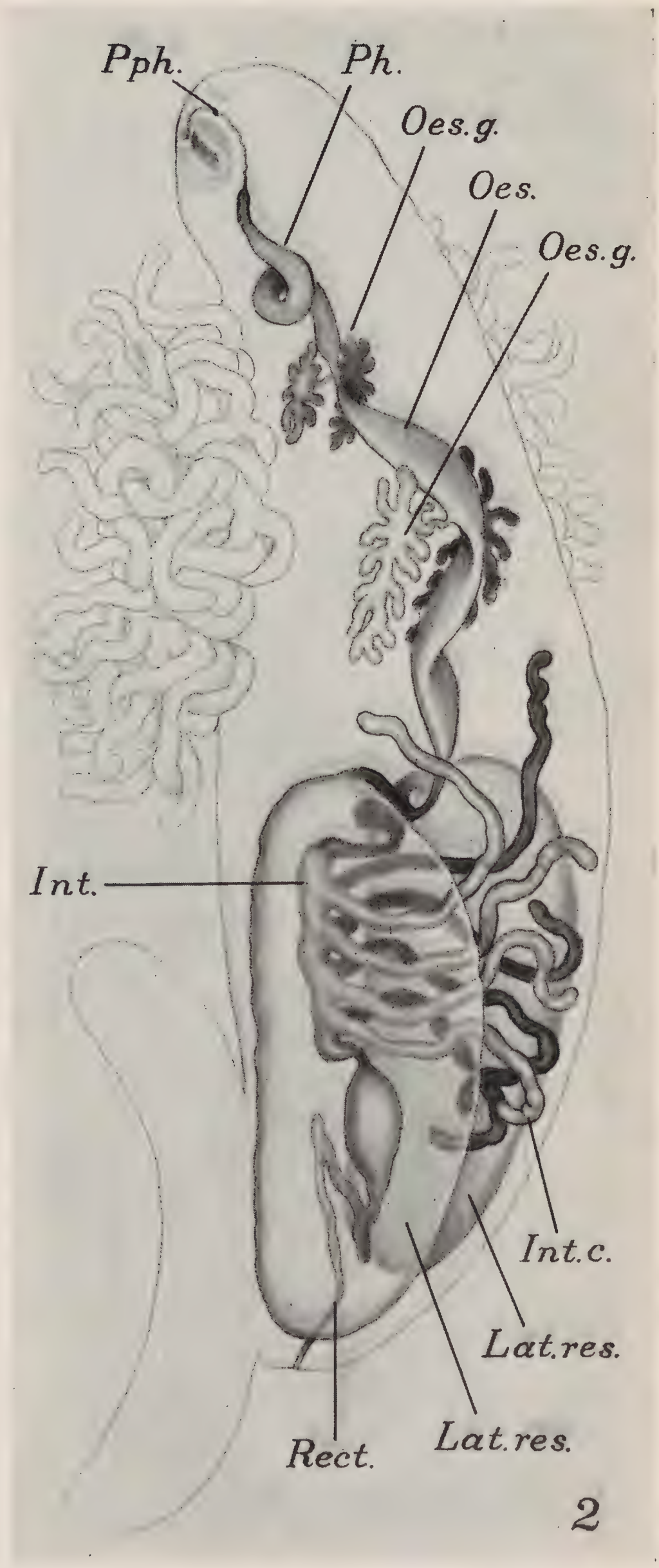


Fig. 1. *Ozobranhus branchiatus*. Ventral surface.

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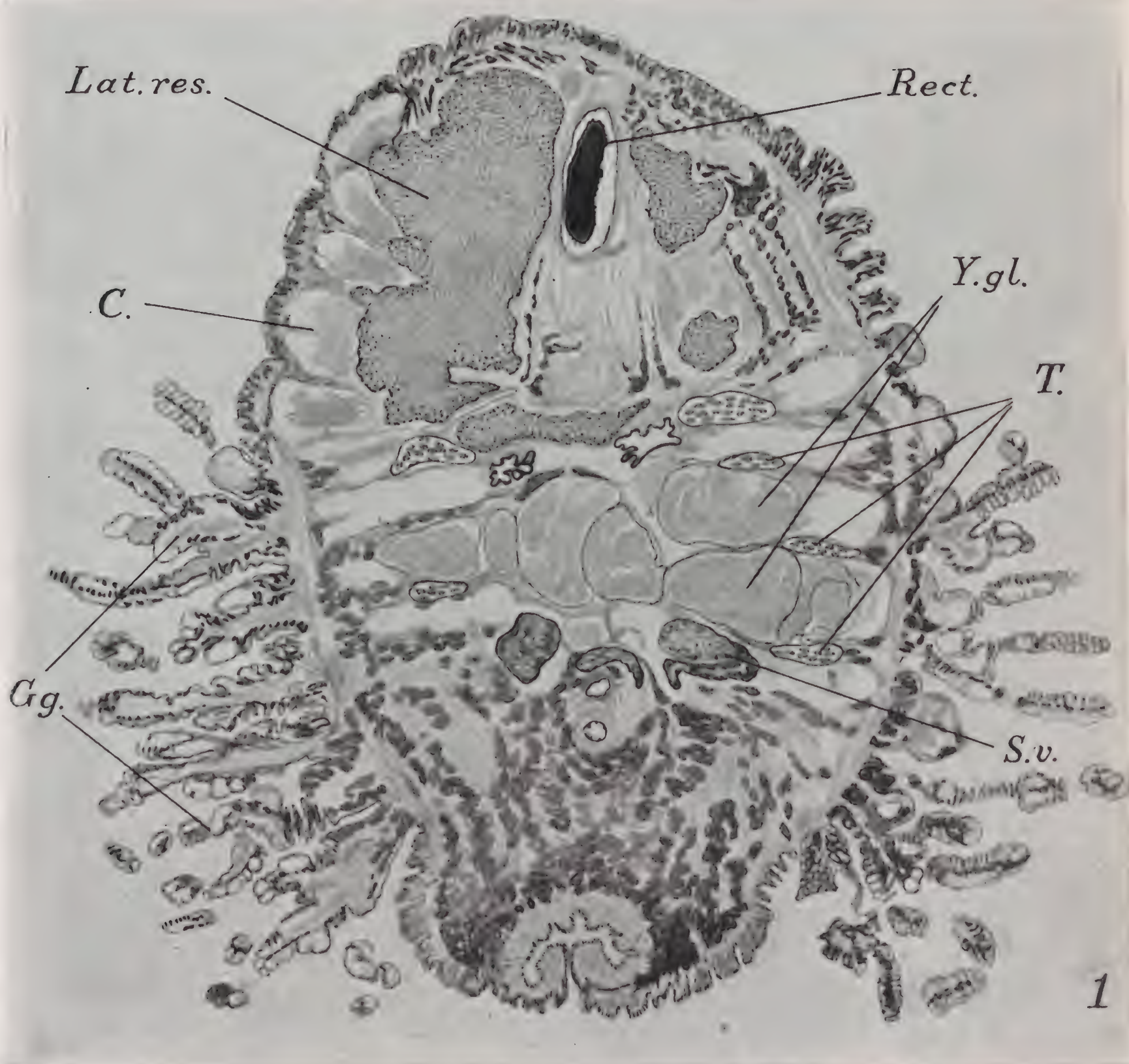
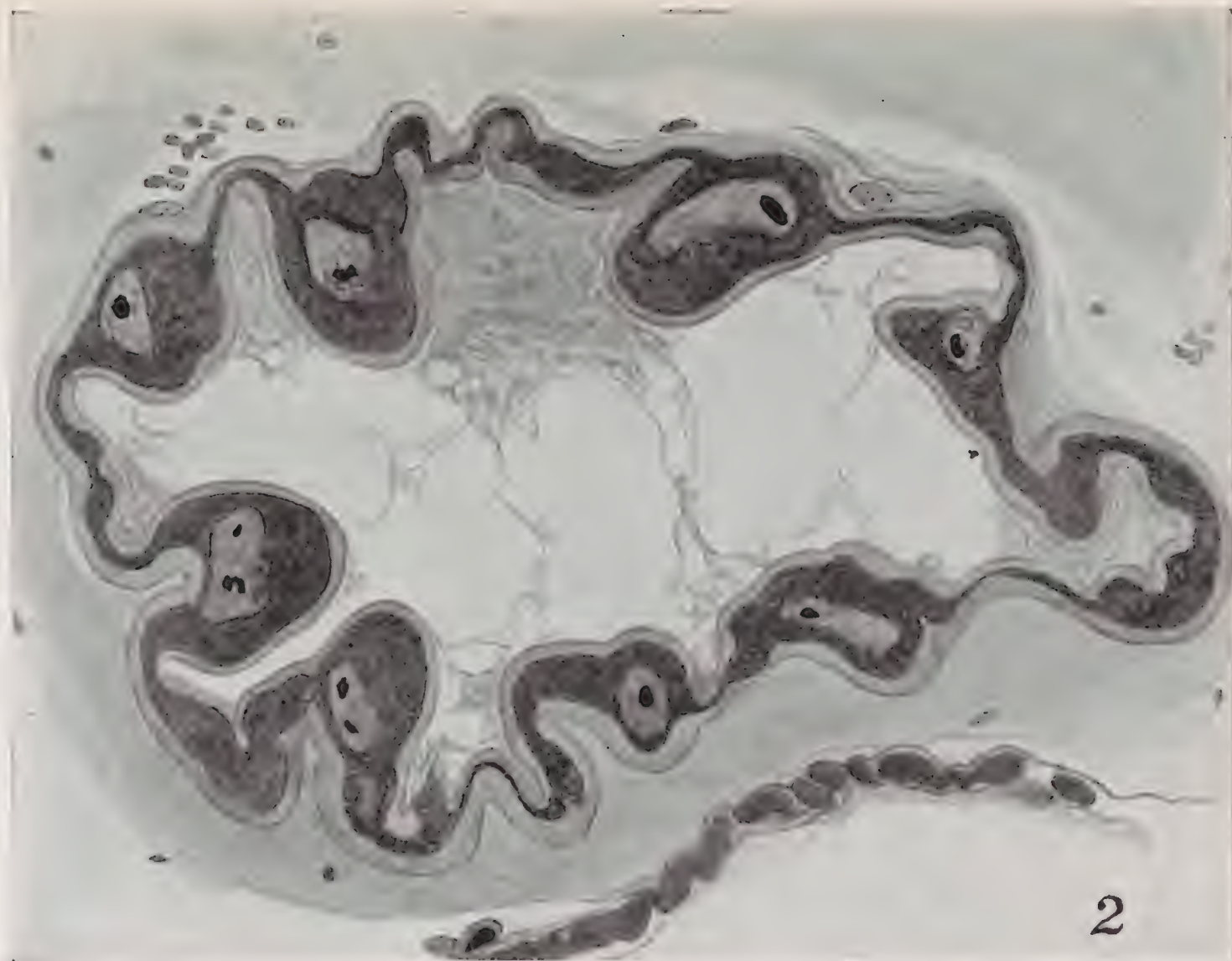
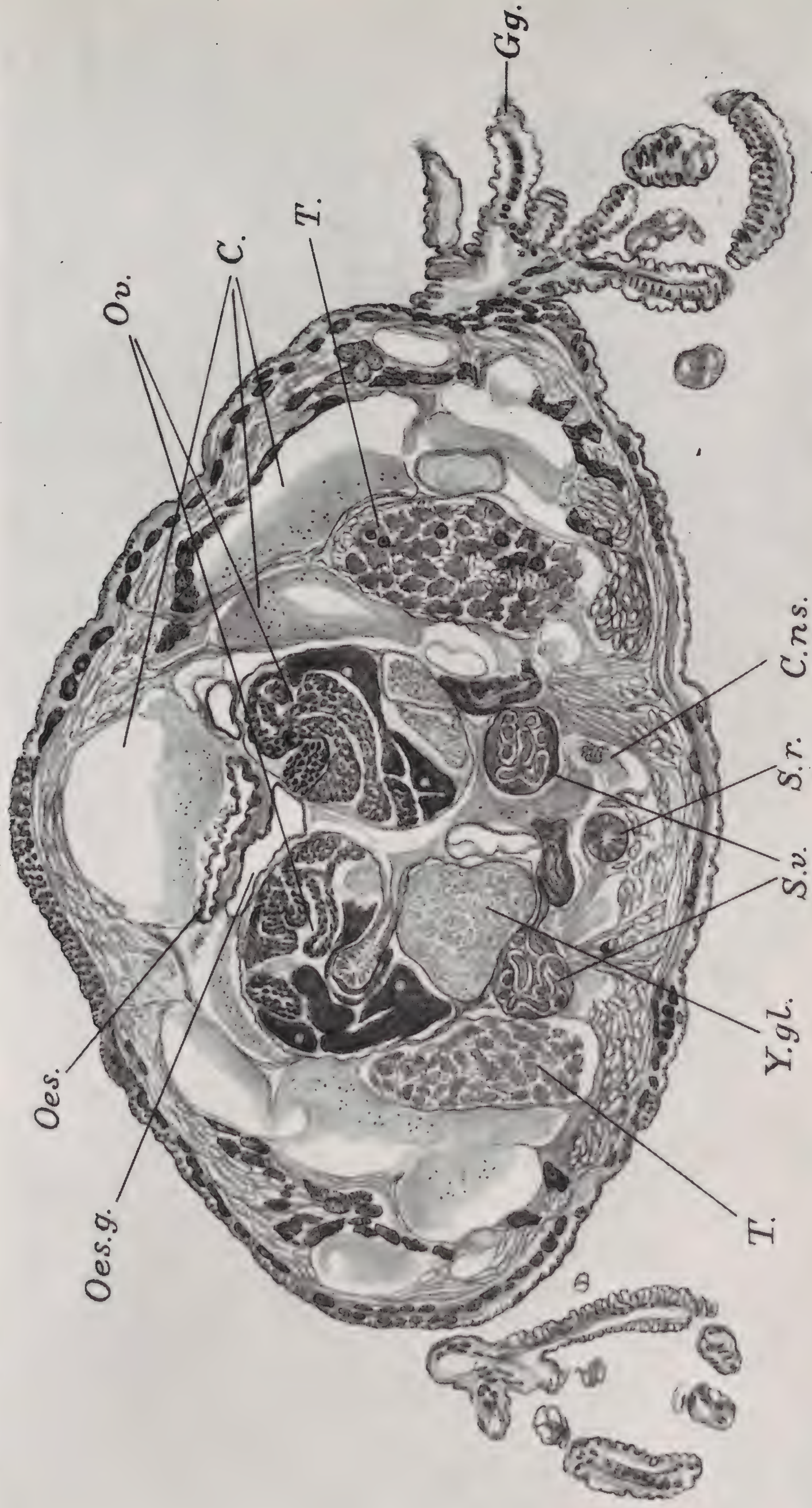


Fig. 1. *O. branchiatus*. Horizontal section. *C.*, sinus filled with blood-like fluid; *Gg.*, seven groups of gill filaments; *T.*, testes; *Y. gl.*, yolk gland; *S. v.*, seminal vesicles; other letters as above.

Fig. 2. *O. branchiatus*. Cross-section of one of the intestinal cœca. Cf. Pl. XXXIII, fig. 2.



O. branchiatus. Transverse section at level of the ovaries. Letters as before; *Ov.*, ovaries; *C. ns.*, ventral gangliated nerve cord; *S. r.*, seminal reservoir.

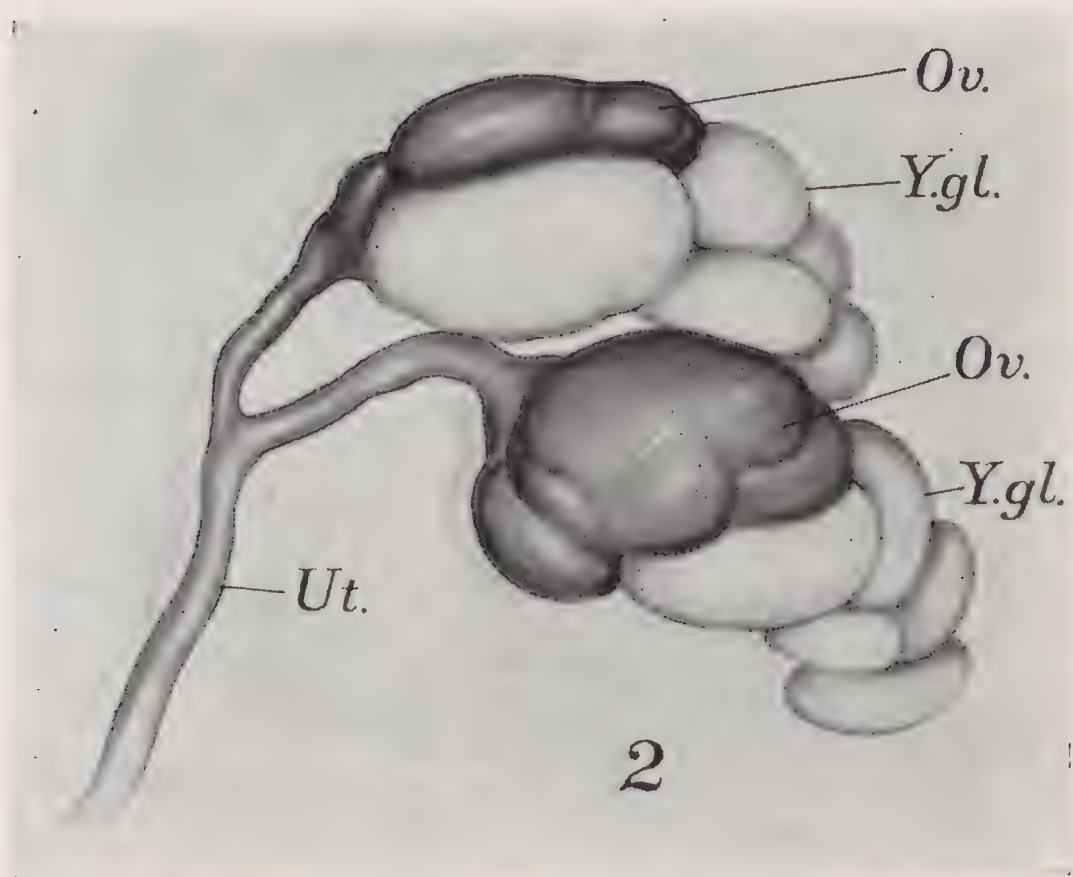
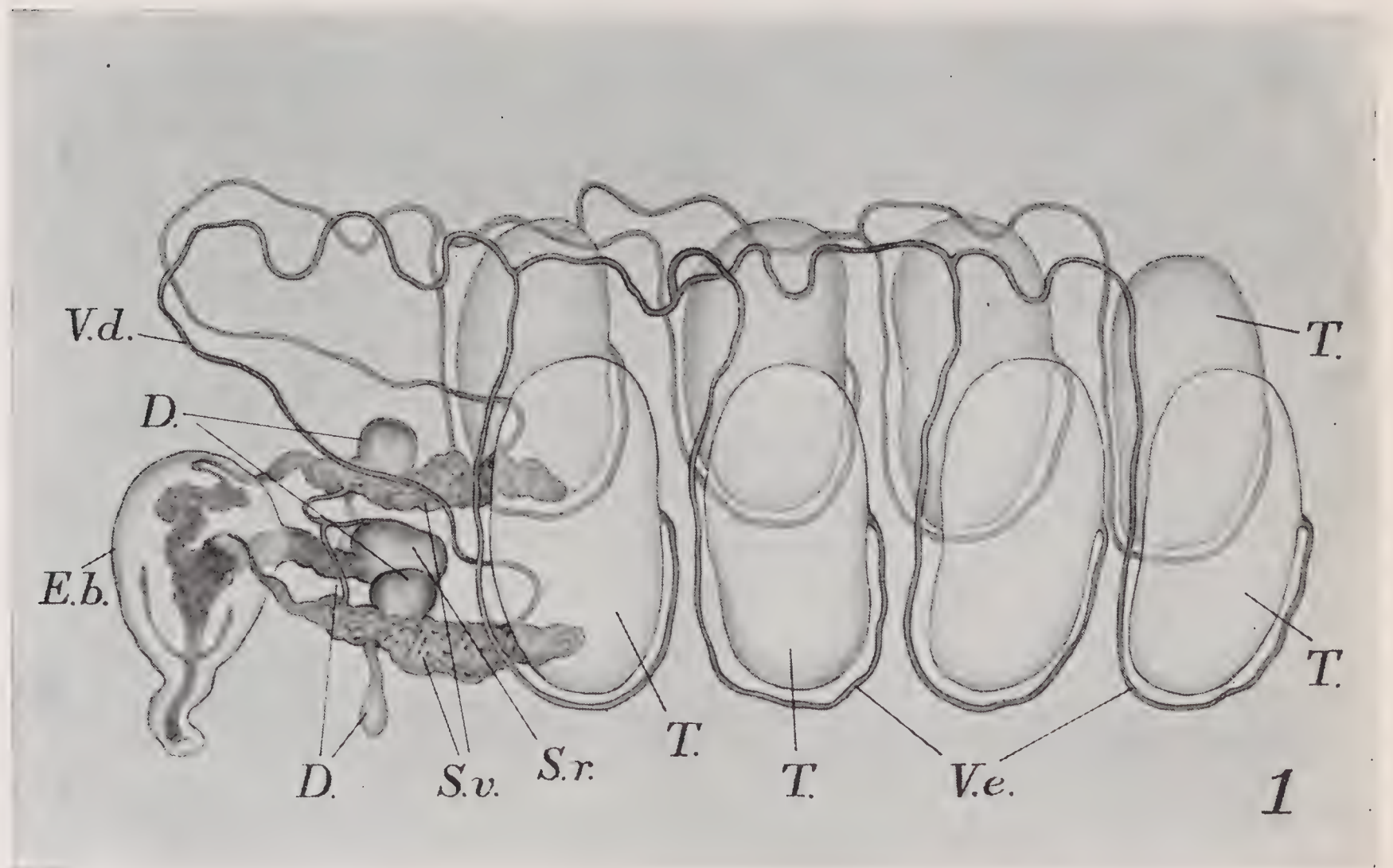


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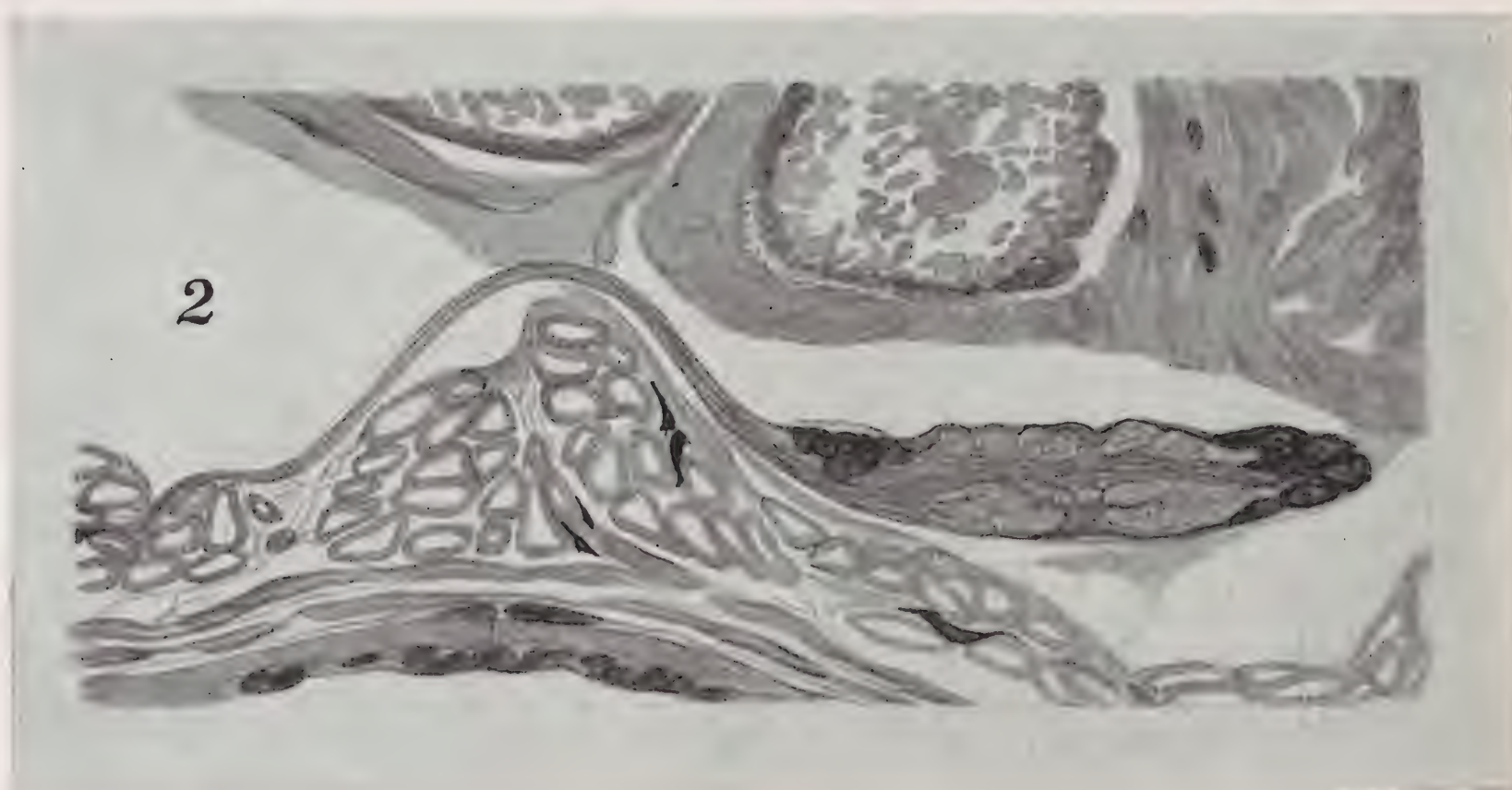


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Figs. 3 and 4. Tactile sense organs on skin of head.

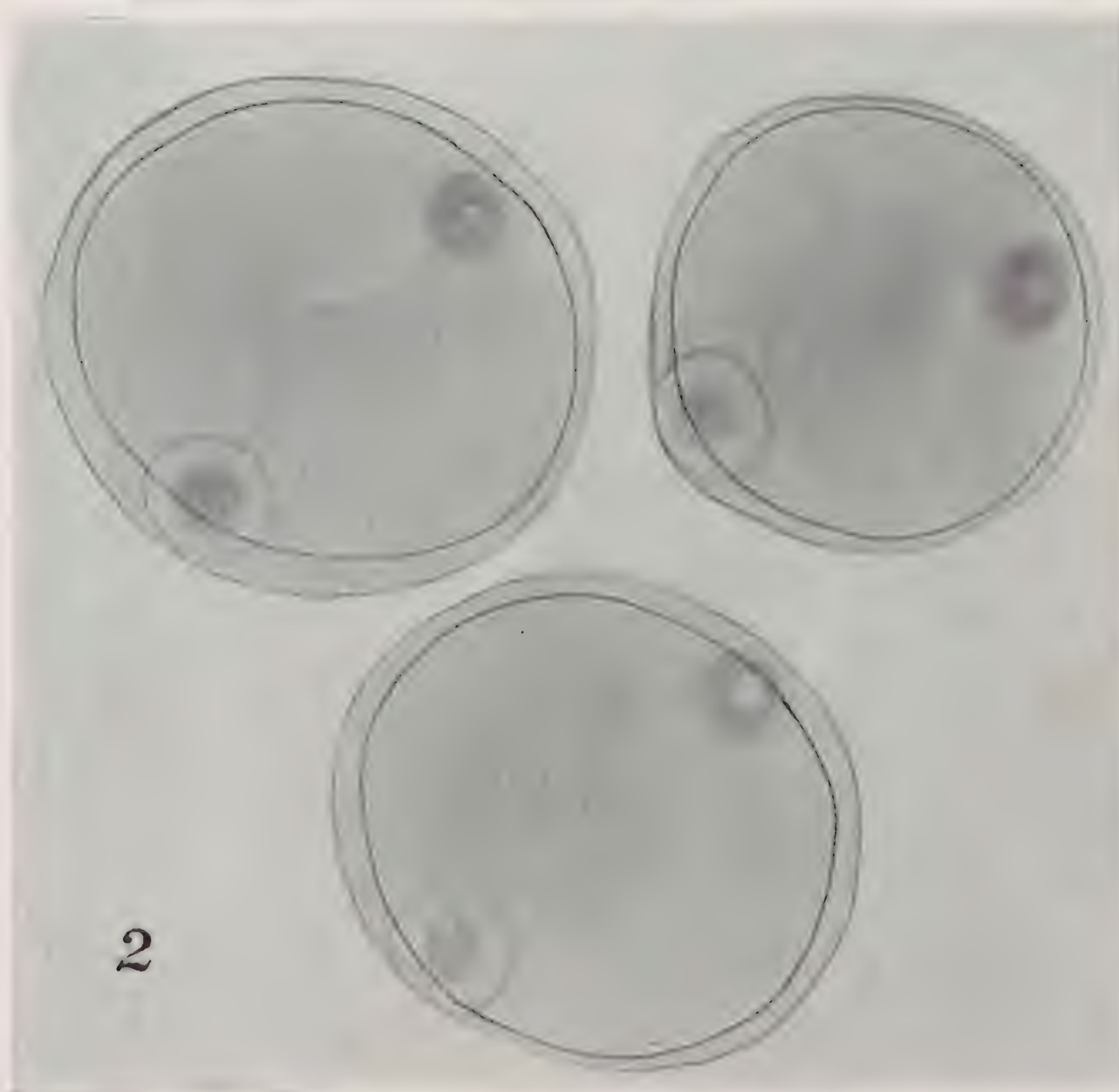


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 Fig. 2. *O. branchiatus*. Eggs from skin of the host.
 Fig. 3. *O. branchiatus*. Young worm showing eyes, rudimentary gills, and undeveloped intestinal tract.

**Article XIII.—THE FISHES OF THE GENUS *ATHERINOPS*,
THEIR VARIATION, DISTRIBUTION, RELATION-
SHIPS, AND HISTORY¹**

BY CARL L. HUBBS

OF THE FIELD MUSEUM OF NATURAL HISTORY

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I.— DISTRIBUTION AND RELATIONSHIPS

The atherinoid fishes of America have become differentiated into a number of generic types, among the most sharply distinguished of which *Atherinops*, the subject of the present paper, may be placed. This genus is characterized by non-protractile premaxillaries and bifid teeth.

The species of *Atherinops*, although very abundant along the West American coast — some of them being food-fishes of good quality and some importance — and although rather frequently mentioned in the literature of the fishes of that region, are at present very imperfectly known. In fact, three of the forms have remained undescribed: *littoralis*, *cedroscensis*, and *guadalupæ*. In all, the genus includes no fewer than seven forms, each inhabiting its separate district along the western coast of the United States and Mexico. The genus has not been recorded within the Tropics nor from Puget Sound.

These seven species and subspecies of *Atherinops* are localized in their distribution to a degree rather unusual among marine fishes. Such a localized distribution is in harmony with their habits. These fishes are very closely restricted to the shore line, those of the continental coast

¹ Based upon material in the American Museum, Stanford University, the National Museum, and the Field Museum. I am particularly indebted to the authorities of the American Museum for the loan of their fine series of specimens from Lower California.

spawning in bays and estuaries, even ascending the mouths of certain streams to fresh water. No such conditions are found on the islands, but the island forms are perhaps confined largely to the more sheltered coves. The fishermen claim that *Atherinopsis californiensis*, a congener of *Atherinops*, migrates back and forth between the northern Santa Barbara Islands and the mainland, while the "Silver Smelt" (*Atherinops*) remains in and about the bays. Just such a situation may hold true, for *Atherinopsis*, of larger size than *Atherinops*, breeds along the mainland in more open waters and seems to be much the stronger swimmer of the two and of less constant occurrence near shore. A single species of *Atherinopsis* occurs along the mainland coast of California, and about the Santa Barbara Islands, and has also been recorded from Cerros Island — the type locality of a very different species, *Atherinopsis sonoræ*.¹

The genus is represented in the Gulf of California by *Atherinops regis*, for which a new genus or subgenus, *Colpichthys*, has recently been proposed in order to distinguish it from *Atherinops* proper. The typical subgenus in its various forms occurs along the outer coast of Lower California, California, and Oregon, and on the adjacent islands. There are three mainland and three island forms, the distribution of which is indicated on the accompanying map: *affinis*, occurring along the coast of Oregon and northern California; *littoralis*, on the mainland coast of southern California; *insularum*, about the adjacent Santa Barbara Islands; *magdalenæ*, in the bays of southwestern Lower California; *cedroscensis*, around Cedros Island off central Lower California; and *guadalupæ*, about Guadalupe Island, farther offshore.

These six forms of the subgenus *Atherinops* differ from one another more or less constantly in several characters, the most important of which seems to be the size of the scales. In a tabulation of the scale counts two groups are indicated (see Table I). The forms from the mainland coast of southern California and Lower California (*littoralis* and *magdalenæ*) have larger scales than those from the offshore islands and those from the northern mainland. In certain other characters, notably the length of the pectoral and the breadth of the head, the southern island forms resemble that one of the northern mainland (*affinis*) more closely than *littoralis* and *magdalenæ* of the shores opposite the islands.

Centering our attention now upon *insularum*, from the Santa Barbara (or Channel) Islands off southern California, we find that it especially resembles *affinis*² of the mainland farther north in the several characters by which it differs from the southern mainland type, *littoralis*. It does,

¹ Osburn and Nichols, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 158, fig. 8.

² The island form, *insularum*, has been contrasted in the literature with *littoralis* on the erroneous supposition that the specimens of the latter form were typical of *affinis*.

indeed, seem remarkable that *Atherinops* should be represented on these several islands by a form well differentiated from the one occurring on the mainland, which is separated from certain of the islands (Santa Catalina, Santa Cruz) by channels narrower than those which separate these islands from others (San Clemente, San Nicholas), the surrounding waters of which are inhabited by the same island species. The situation is further unusual in that the island species is related more closely to a form of a relatively distant mainland, that of central California, than to the form of the neighboring mainland shores. Some past migration of the species concerned must apparently be postulated to account for the relationships of these fishes. The discussion of this subject will be deferred, however, to a later section of this paper.

The Cedros Island and the Guadalupe Island forms, as already indicated, resemble *insularum* and *affinis* rather than the southern mainland types in several characters: their relatively fine scales; their short pectorals; their broader heads, etc. They further resemble *insularum* very closely in the form of the body. In certain other characters, however, they approach the southern mainland forms (see comparative tables). Of the two southern island forms, *guadalupæ* is the more distinct, many of its characters contrasting with those of *insularum*. In nearly all of these characters (see tables) *cedroscensis* is intermediate between the other two island types; it also seems to approach the adjacent mainland race in one character, the width of the head. Despite the resemblances between the southern island and the southern mainland forms, it is highly probable that the *Atherinops* of both Cedros and Guadalupe Islands, though separated from each other by a wide distance and by deep water, are related most closely to *affinis* through *insularum*, rather than with the form occurring on the mainland coast of Lower California.

II.—SUBSPECIFIC INTERGRADATION

A very large series of specimens¹ from representative localities along the California coast from San Francisco to San Diego has made possible a detailed study of the relations between *affinis* and *littoralis* where their ranges meet. Although the two forms are well distinguished by numerous characters, they have been found to intergrade throughout a rather wide area, extending from northern San Luis Obispo County to Point Arguello; even the series from the mainland shores of the Santa Barbara Channel show a definite approach toward *affinis* in several characters.

The series of intergrades between *affinis* and *littoralis* can always be distinguished from either form by the summation of the various distinctive

¹ Collected by the writer to determine the inter-relationships of *affinis* and *littoralis*.



TABLE II.—THE GEOGRAPHICAL VARIATION IN THE NUMBER OF TRANSVERSE SCALE-ROWS IN THE SUBSPECIES OF *Atherinops affinis* (COMPARE WITH TABLE I)

Transverse Scale-rows		52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
<i>affinis</i>	OREGON south to MONTEREY BAY																	
	Yachats R., Oregon.....																1	...
	Drakes Bay, Cal.....															1	...	...
	San Francisco Market.....								1	6	2	4	4	3	2	2	...	1
	Santa Cruz, Cal.....										1	...		2	1	...	...	...
<i>affinis</i> × <i>littoralis</i>	CENTRAL CALIFORNIA (south of Monterey Bay)																	
	Near Piedras Blancas.....										2	...					...	...
	Morro Bay.....					1	2	2	2	4	6	...		1	1		...	1
	Avila, near Port San Luis.....			1		3	3	5	5	5	3	2	4	2			...	...
	Lagoon at Surf (Lompoc Junction).....					1	1	1	2	2	2	2	...	1			...	...
<i>littoralis</i> varying toward <i>affinis</i>	SANTA BARBARA CHANNEL																	
	Estero at Goleta.....		1			1	5	1	2	...	1	1	1	1	1		...	...
	Santa Barbara.....						1	...	...			...					...	...
	Estero at Carpenteria.....			1	3	1	3	3	3	1	...	1	...				...	...
<i>littoralis</i>	SOUTHERN CALIFORNIA																	
	Ventura.....					1												...
	Alamitos Bay.....		1			1												...
	San Diego Bay.....	1	3	2	5	6		4										...
<i>littoralis</i> × <i>magdalenæ</i>	CENTRAL LOWER CALIFORNIA																	
	San Bartolomé Bay.....				2		4	1										...
<i>magdalenæ</i>	SOUTHWESTERN LOWER CALIFORNIA																	
	Magdalena Bay.....	5	2	4	5	4	2	2										...

Number of Specimens

characters. Most of the specimens combine in various ways the characters of the two contrasted forms.¹ Thus, some specimens have scales fully as large as in typical *littoralis*, but resemble *affinis* in the wide interorbital and deep caudal peduncle. In the mode of their variation, however, most of the characters of these intergrades are intermediate between those of *affinis* and those of *littoralis*. As an example, the size of the scales may be taken (see Table II). Other characters in which these intergrades are notably intermediate are: the interorbital width (Table XV); the length of the pectoral fin (Table XIX); the depth of the caudal peduncle (Table III); the length of the eye (Table XVII); the length of the head (Tables XIII and XIV); and, finally, the size (Table VIII) and general appearance. In no respect, so far as examined, do the intergrades resemble either *affinis* or *littoralis* exclusively. The intergrades, in fact, are intermediate in all respects; or, expressed more definitely, they may resemble both *affinis* or *littoralis* in the characters in which these forms differ from each other.

In similar fashion, specimens of *Atherinops* from middle Lower California (San Bartolomé Bay) are intermediate between *littoralis*, which is abundant farther north, and *magdalenæ*, known only from the vicinity of Magdalena Bay, farther south. The chief difference apparent between *magdalenæ* and *littoralis* is the depth of the caudal peduncle, in which character the Magdalena Bay form resembles typical *affinis*. In both cases the intergrades are intermediate.

TABLE III.— THE DEPTH OF THE CAUDAL PEDUNCLE (MEASURED INTO THE HEAD),
IN THE SUBSPECIES OF *Atherinops affinis*

	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2
<i>A. a. affinis</i>										
Intergrades										
<i>A. a. littoralis</i>										
Intergrades										
<i>A. a. magdalenæ</i>										

These intergrades between *littoralis* and *magdalenæ* seem to have rather wider interorbitals, on the average, than typical examples of either form,

¹ A similar situation occurs in the case of *Menidia m. menidia* on the Atlantic Coast (see Kendall, 1901, Rept. U. S. Fish Comm. (1902), pp. 241-267); the writer has been able to confirm this work of Dr. Kendall.

in this respect resembling *A. i. cedroscensis* from the adjacent Cedros Island; in the few other respects by which *littoralis* and *magdalenæ* differ slightly, the intergrades are apparently intermediate, and show no special approach toward *cedroscensis*.

To sum up the interrelationships of the three mainland forms of *Atherinops*, it may be said that specimens from the two areas where the ranges of the forms meet are either intermediate in nearly every character between the subspecies occurring on the two sides; or, more usually, variously combine their characters. Especially in the case of *affinis* and *littoralis* is there evident an actual intergradation of the two forms. In this case the intergradation suggests hybridization rather than uniform blending.

III.—PHYLOGENY

In the foregoing sections an outline of the distribution and relationships of the species and subspecies of *Atherinops* was presented. Some rather anomalous features were indicated, which call for an explanation. The main question to answer is, why does the form (*A. i. insularum*) living about the Santa Barbara Islands, close off southern California, resemble more closely a form (*A. a. affinis*) of the northern California coast than the form found along the mainland near-by. The similarity of *A. a. affinis* and *A. i. insularum* is so close that one is justified in postulating that their separation has been shorter than that of *A. i. insularum* and *A. a. littoralis* of the adjacent mainland. *A. a. littoralis* is separable only by very minor characters from *magdalenæ* of the Lower California mainland coast. The differences which distinguish *insularum* from *littoralis* are mostly paralleled by those distinguishing *cedroscensis* from *magdalenæ*; and *cedroscensis* in its distinctive characters differs only in the mode of its variation from *insularum*. *A. i. guadalupæ* approaches the southern mainland type (*littoralis*) in several of its characters, but the small size of its scales, the breadth of its head, its form, color, etc., seem fully to justify its inclusion in the island series. The *Atherinops* of all the southern islands, therefore, are apparently related most closely to *A. a. affinis* of the mainland to the north and have probably been separated from it by no long period of time. Since the island forms have become isolated from *affinis*, however, considerable differences in each have developed. Three island varieties have become differentiated, but all three have retained certain features by which they differ from *A. a. affinis*; hence, the northern mainland form appears also to have become modified. How the southern islands, now separated from one another by wider distances and deeper channels than those which separate some of the islands from the mainland, could become populated by the northern, rather

than the southern, mainland form is not at first apparent. One might postulate that the young of the northern form, swept out of the bays by the tidal currents, were carried south by the prevalent southward surface drift and by this means reached the islands; or that the adults, contrary to their present habits, at one time forsook the northern coasts and swam southward to the islands. Had such a transfer been made, the original stock would have come, in all probability, from the coastline not far north or east of Point Conception (see map), but the races of *Atherinops* in those districts are not *A. a. affinis*, as such a theory would demand, but intergrades between that form and the dissimilar *A. a. littoralis*. The fact that the southern island form has remained distinct from the southern mainland forms, while the widely separated islands are populated by the same species (of three varieties, one of which inhabits all of the Santa Barbara Islands), would further indicate that some other means of species dissemination has taken place.

A study of the diastrophic movements to which the California coast has been subject seems to afford a plausible explanation of the distribution of the forms of *Atherinops*. During the so-called post-Miocene uplift, the California coast south of San Francisco was elevated to a great height above its present level. At Monterey the elevation probably amounted to not less than one mile, for the great submerged valley of Monterey may be traced out to a depth of about 1000 fathoms. As the 500 fathom contour line is found to enter sharply a number of such submerged valleys, where the soundings have been extensive (in Monterey Bay, off San Diego, etc.), it may safely be concluded that this coast region as a whole was elevated to a greater height than 3000 feet.¹ The 500 fathom contour probably represents the approximate location of the shore-line of the coast at some post-Miocene period, although differential diastrophic movements, particularly of the islands, may introduce a considerable error. The present islands were then apparently peninsulas surrounding large arms of the sea.

The time of the uplift just referred to has been given by several geologists² as Pliocene, but Branner,³ by synchronizing this elevation with the glaciation of the Sierra Nevada Mountains, more recently considers the uplift of Pleistocene age. The occurrence of Mastodon remains on the Santa Barbara Islands points to the same conclusion, namely, that the Santa Barbara Islands were connected with the mainland during a cold period of Pleistocene times. A more southern distribution of most of the cen-

¹ The Coast Survey Charts of California, on which many additional soundings by the *Albatross* and by the Scripps Institution for Biological Research were located, formed the basis for the construction of a map, upon which these statements are based.

² See for example Lawson, Bull. Dept. Geol., Univ. Cal. (several papers, Vols. I-III).

³ 1907, Journ. Geol., XV, pp. 1-10, fig.

tral California fishes was probably a feature of that period. *Atherinops affinis*, or rather its immediate ancestor, may then be supposed to have ranged farther southward than at present. Under such conditions it would have occurred around the shores of what are now the southern islands (except Guadalupe). The great inclosed bays between the mountain ranges, which then represented the present Santa Barbara Islands, may well have teemed with this *Atherinops* — the ancestor of *A. a. affinis* and of the three varieties of *A. i. insularum*. The channel between Guadalupe Island and the mainland to the north, at the time of the great uplift, about one-half or one-third narrower than at present, was probably crossed by this ancestral *Atherinops*.

This fine-scaled ancestor of *A. a. affinis* and of the varieties of *Atherinops insularum* during this cold period would have occupied the mainland parallel to that now inhabited by the two large-scaled forms. Now, subsequent to this great elevation there occurred a depression which carried the coast line of the southern half of California downward to a depth of from 800 to 1500 feet¹ below the present level. This depression was obviously accompanied by a warmer climate, approximating that of the present. This warmer climate presumably acted as a stimulus for a northern migration of the finer-scaled type of *Atherinops* to its present range along the coast of Oregon and the northern half of California. During the subsidence the present islands were detached from the mainland, and it may be supposed that a population of the finer-scaled *Atherinops* was thus trapped about each island. Since their separation, probably in Pleistocene but possibly in Pliocene times, the four forms of this finer-scaled group, thus isolated, have become differentiated sufficiently so as to be distinguishable from one another.

We have now accounted, apparently quite plausibly, for the past history of the finer-scaled forms of *Atherinops* and for their present distribution on the northern mainland and the southern islands. We have yet to consider the coarser-scaled or southern-mainland forms, *magdalenæ* and *littoralis*. To account for the differences between these forms and typical *affinis* of the mainland farther north on the assumption that their differentiation has been synchronal with that of the island forms does not adequately explain the present relationships of the island and mainland forms and, particularly, does not explain satisfactorily the nature of the intergradation between *littoralis* of the southern mainland and *affinis* of the northern mainland. These intergrades, as already explained, usually show the characters of both forms in various combinations: a specimen with scales as large as in typical *littoralis* has the interorbital as wide, and the caudal

¹ As indicated by the height of the marine terraces, as given by Lawson (*loc. cit.*).

peduncle as deep, as in typical *affinis*, etc. The intergradation, in fact, suggests hybridization, rather than the differentiation of a previous unit in the two extremes of distribution.

It seems probable, on the basis of the full evidence available, that the coarser-scaled type of *Atherinops*, subsequent to the northward migration of the finer-scaled type and to the separation of the southern islands from the mainland, has likewise moved northward, meeting the finer-scaled type on the central coast of California. By the interbreeding of the two forms in this region the peculiar hybrid-like intergrades have probably arisen. Now, if this intergradation should spread more widely, or if the typical form on either side should become extinct or differentiated, then, according to the above explanation, we should have a *synthetic species* produced not by divergence but rather by the fusion of two species which were formerly distinct.

IV.—NOTES ON, AND DESCRIPTIONS OF, THE SPECIES

The genus *Atherinops* is distinguished from all other atherinids by its bifid or Y-shaped teeth; in other characters it closely resembles *Atherinopsis*, another genus of the western coast of North America. *Atherinops* is divisible into two subgenera, *Colpichthys* and *Atherinops*.

Subgenus **COLPICHTHYS** Hubbs

Colpichthys HUBBS, 1918, Proc. Acad. Nat. Sci. Phila., LXIX, p. 305.

This subgenus, which with its single species represents *Atherinops* in the Gulf of California, has recently been described in sufficient detail.

1. *Atherinops regis* Jenkins and Evermann

Atherinops regis JENKINS AND EVERMANN, 1888, Proc. U. S. Nat. Mus., XI, p. 138 (Guaymas). EVERMANN AND JENKINS, 1891, idem, XIV, p. 137 (Guaymas). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807 (Gulf of California).

Range.—Gulf of California.

Record-station.—Guaymas, Sonora, Mexico.

Relationships.—The only species of the subgenus *Colpichthys*.

Habits.—Unrecorded.

Measurements and Counts (taken from five of the type specimens, varying in length to caudal from 95 to 150 mm.).—Length of head into total length to caudal, 4.0 to 4.55; depth of body, 4.0 to 4.5; depth of caudal peduncle into length of head, 2.25 to 2.5; length of snout, 3.4 to 3.5; length

of upper jaw, 3.3 to 3.85; diameter of eye, 3.5 to 3.8; least width of interorbital, 2.9 to 3.1; length of head into distance from isthmus to anus, 1.8 to 1.95. Measurements in hundredths of length to caudal base: head, 22.2 to 24.5; depth of body, 22.5 to 25; depth of caudal peduncle, 10; length of snout, 6.7 to 7.5; upper jaw, 6 to 7.6; eye, 6 to 7; interorbital, 7.8 to 8.2; isthmus to pelvic fin, 29.6 to 32.6; tip of snout to dorsal fin, 53 to 57; snout to pelvic fin, 44 to 48.5; pelvic fin to anus, 12.3 to 12.7; anus to base of caudal, 42 to 44; length of first dorsal fin when depressed, 9.3 to 11; distance between origins of dorsal fins, 15.3 to 18.4; base of second dorsal, 10 to 12; height of second dorsal, 12; base of anal, 21.5 to 23; end of anal base to base of caudal, 17 to 18.5; pectoral fin, 26; pelvic fin, 12. Number of spines in first dorsal, 5 to 7; soft rays of second dorsal, 10 or 11; soft rays of anal, 20 to 22; rays of pectoral, 14 or 15; transverse scale-rows, 47 to 51.

Subgenus **ATHERINOPS** Steindachner

Atherinops STEINDACHNER, 1875, Sitzb. Akad. Wiss. Wien, LXXII, part 1, p. 89 (1875, Ichth. Beit., III, p. 61). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807.

The typical subgenus includes six species, subspecies, and island varieties, occurring along or off the coast of Oregon, California, and Lower California.

2. *Atherinops affinis affinis* (Ayres)

Atherinopsis affinis AYRES, 1860, Proc. Cal. Acad. Nat. Sci., p. 63 (San Francisco).

Chirostoma affine GILL, 1862, Proc. Acad. Nat. Sci. Phila., p. 280 (after Ayres).

Atherinops affinis STEINDACHNER, 1875, Sitzb. Akad. Wiss., Wien, LXXII, p. 89.

JORDAN AND GILBERT, 1880, Proc. U. S. Nat. Mus., III, (1881), p. 456 (San Francisco; Monterey Bay). JORDAN AND JOUY, 1881, idem, IV, p. 13 (San Francisco). JORDAN AND GILBERT, 1881, idem, IV, p. 43 (in part; "Cape Mendocino southward"); 1883, Bull. U. S. Nat. Mus., XVI, p. 409 (in part; "Pacific Coast"). EIGENMANN AND EIGENMANN, 1892, Ann. N. Y. Acad. Sci., VI, p. 352 (Monterey; San Francisco). GILBERT, 1893, Rept. U. S. Fish Comm., (1896), p. 465 (Drake Bay). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807 (in part; "Coast of California"). GILBERT, 1898, Rept. U. S. Fish Comm., (1899), p. 25 (Monterey). STARKS AND MORRIS, 1907, Univ. Cal. Publ. Zool., III, p. 187 (in part; "San Francisco to Magdalena Bay"). EVERMANN AND LATIMER, 1910, Proc. Biol. Soc. Wash., XXIII, p. 136 (Tomales Bay).

Atherinops insularum GILBERT, 1893, Rept. U. S. Fish Comm., (1896), p. 465 (Drake Bay). Not *Atherinops insularum* GILBERT, 1891.

Atherinops regis EVERMANN AND LATIMER, 1910, Proc. Biol. Soc. Wash., XXIII, p. 136 (Tomales Bay). Not *Atherinops regis* JENKINS AND EVERMANN, 1891.

Atherinops oregonia JORDAN AND SNYDER, 1913, Proc. U. S. Nat. Mus., XLV, p. 575, Pl. XLVI (Yachats River, Oregon).

Range.—Coast of Oregon, and of California, south to Monterey.

Record-stations.—Yachats River (near mouth), Lincoln County, Oregon: Jordan and Snyder, as *Atherinops oregonia*. Tomales Bay, California: young recorded by Evermann and Latimer as *Atherinops affinis* and *Atherinops regis*. San Francisco: recorded by Ayres, and by authors in general (usually from the market). Monterey Bay: recorded by Jordan and Gilbert. Santa Cruz: specimens collected by Dr. C. H. Gilbert. Monterey: recorded by Gilbert.

Habits.—*A. a. affinis* is a common fish in the bays and is recorded as entering fresh water (Yachats River, Oregon) in the spawning season.

Nomenclature.—*Atherinops affinis* (Ayres) is the type species of its genus and was the first to be described. Although a common market fish at San Francisco, it seems not to have been well represented in collections, a condition which has led to considerable confusion. Thus, *Atherinops insularum* Gilbert was distinguished in the original description from *A. a. littoralis*, on the assumption that the specimens of that subspecies examined were typical of *A. affinis*, whereas in reality *insularum* is less distinct from typical *affinis* than *littoralis* is; subsequently, typical specimens of *A. a. affinis* were recorded by Dr. Gilbert as *insularum*, and doubt was then expressed as to the validity of the island form. In somewhat similar fashion, the type of *Atherinops oregonia* was contrasted with *A. a. littoralis*, and the identity of *oregonia* with true *affinis* was consequently not appreciated.

The type description of *Atherinopsis californiensis* by Girard¹ agrees better with *Atherinops affinis* than with the species currently known under Girard's name; and, as both species are common in the San Francisco markets, a difficult nomenclatural problem is suggested. Fortunately, however, Mr. Fowler² has redescribed the type of *Atherinopsis californiensis*, showing that there has been no error in the current application of that name.

TABLE IV.—MEASUREMENTS AND COUNTS OF *Atherinops affinis affinis*

	Yachats River ^a	Drakes Bay ^b	San Francisco Markets ^c	Santa Cruz
Number of specimens examined.	1	1	14	4
Length to base of caudal, mm.	227	164	130 to 156	105 to 134
Length of head in body.	...	5.33	4.8 to 5.6	4.75 to 5.0
Depth of body.	...	5.25	... to 5.33	4.4 to 4.9
Depth of caudal peduncle in head.	...	2.6	2.33 to 2.7	2.5 to 2.6
Length of snout.	...	3.3	3.4 to 3.7	3.4 to 3.7

¹ 1854, Proc. Acad. Nat. Sci. Phila., VII, p. 134.
² 1903, idem, (1904), p. 739.
^a Measurements from type description or type figure of *A. oregonia*.
^b Specimen recorded by Gilbert as *A. insularum*.
^c Measurements made from the entire series only in the case of the critical characters.

TABLE IV (continued)

	Yachats River ^a	Drakes Bay ^b	San Francisco Markets ^c	Santa Cruz
Length of upper jaw.....	...	3.75	3.6 to 4.0	3.4 to 3.7
Length of eye.....	...	4.4	3.9 to 4.4	3.7 to 4.1
Width of interorbital.....	...	3.25	2.95 to 3.2	3.0 to 3.25
Length of postorbital.....	...	2.18	2.15 to 2.2	2.15 to 2.25
Length of head in distance from isthmus to anus.....	2.7	2.4	2.4 to 2.8	2.35 to 2.55
<i>Measurements in hundredths of length to caudal base</i>				
Length of head.....	18	19	17.8 to 20.5	20.2 to 21.8
Depth of body.....	22	20		21 to 23
Depth of caudal peduncle.....	8	7.8	7.8	7.8 to 8.3
Length of snout.....	5	6	5.3 to 5.6	5.8 to 6
Length of upper jaw.....		5.3	4.8 to 5.2	5.6 to 6
Length of eye.....	4	4.4	4.6	5 to 6
Width of interorbital.....		6.2	6.1 to 6.2	6.5 to 7.3
Length of postorbital.....		9	8.2 to 9.2	9 to 9.8
Distance, snout to dorsal fin.....		62	57.7 to 59.3	57.7 to 61
“ snout to pelvic fin.....	40	42.3	45.3	45.5 to 46.7
“ isthmus to pelvic fin.....		28.6	31.7 to 34.7	32.5 to 33.3
“ anus to pelvic fin.....	18	16.8	15.7 to 18.5	15.5 to 17.5
“ anus to base of caudal... 42.3	40	42		39.4 to 42
Length of first dorsal, depressed.....	8	7.2	6.6 to 8.2	6.6 to 7.8
Distance between origins of dorsals..	14.8	12	12.8 to 16.2	12 to 13.4
Length of second dorsal base.....	11.4	10.5	9.2 to 10.2	10 to 10.8
Height of second dorsal fin.....			9.8 to 10.2	10.2
Length of base of anal fin.....		19	18.4 to 20.8	19.3 to 21.2
Length of caudal peduncle.....		18	17.8 to 19	16.5 to 18
Length of lower caudal lobe.....			19.4 to 24	
Length of pectoral fin.....		19	18 to 21	19.5 to 20.2
Length of pelvic fin.....		9.3	8.7 to 9.6	9.5 to 11
Number of rays: first dorsal.....	VI	V	V to VII	V or VI
“ “ “ second dorsal.....	12	I, 11	I, 9 to I, 12	I, 10 to I, 12
“ “ “ anal.....	24	I, 19	I, 19 to I, 24	I, 20 to I, 23
“ “ “ pectoral.....		14	13 to 15	13 or 14
Number of transverse scale-rows....	67	66	59 to 68	61 to 65

2a. Intergrades between **A. affinis affinis** and **A. affinis littoralis**

Atherinops affinis JORDAN AND GILBERT, 1880, Proc. U. S. Nat. Mus., III, (1881), p. 456 (San Luis Obispo, i. e., Port San Luis, then called Port Hartford). EIGENMANN AND EIGENMANN, 1892, Ann. N. Y. Acad. Sci., VI, p. 352 (Port Hartford). Records only.

^a Measurements from type description or type figure of *A. oregonia*.
^b Specimen recorded by Gilbert as *A. insularum*.
^c Measurements made from the entire series only in the case of the critical characters.

Range.—Coast of central California (San Luis Obispo County, and Santa Barbara County north of Point Arguello).

Record-stations.—Near Piedras Blancas, between that point and San Simeon: young specimens caught in a rock-pool at low tide, on June 2. Morro Bay: spawning adults seined from sand-bar at mouth of Morro Creek, on June 8. Port Hartford: Jordan and Gilbert, as *Atherinops affinis*. Avila, near Port San Luis, which is the present designation of "Port Hartford": spawning adults seined in the brackish water lagoon, and in the fresh water of San Luis Creek near its mouth; May 25–26. Surf (Lompoc Junction): adults seined in the brackish water lagoon at the mouth of Santa Inez River.

Relationships.—The intergradation of *affinis* and *littoralis* has already been discussed (see p. 412): in this connection there need only be added the following series of measurements and counts.

Habits.—This intermediate race of *A. a. affinis* is very abundant, close inshore, along the coast of central California. It is said by the fishermen to enter the bays and estuaries in large numbers in the spring. It spawns in spring or early summer, in or near the mouths of streams. Thus, it was found in Morro Bay spawning on a sand-bar at the mouth of Morro Creek; it was found at Avila to be excessively abundant in the lagoon at the mouth of San Luis Creek, where many hundreds of specimens, including breeding adults, were caught in a single pull of a small minnow-seine; breeding adults were also taken in the fresh water of this creek near its mouth, but not above tide-water; other adults were taken in the brackish water lagoon at the mouth of Santa Inez River. This fish has no great tenacity of life, many of those caught in the minnow-seine dying in the bag while the seine was being drawn a short distance to shore.

Measurements and Counts of ten specimens, 101 to 166 mm. long to caudal, from the mouth of San Luis Creek.—Length of head into total length without caudal, 4.7 to 5.0; depth of body, 4.4 to 5.1; depth of caudal peduncle into head, 2.6 to 3.1; length of snout, 3.4 to 3.6; length of upper jaw, 3.4 to 4.0; diameter of eye, 3.65 to 4.1; width of interorbital, 3.1 to 3.5; length of postorbital, 2.2 to 2.5; length of head into distance from isthmus to anus, 2.1 to 2.4. Measurements in hundredths of length to caudal base: length of head, 20 to 21; depth of body, 20.5 to 22.5; depth of caudal peduncle, 7.2 to 7.8; length of snout, 5.6 to 6.1; upper jaw, 5 to 6.2; eye, 4.8 to 6; interorbital, 6.2 to 6.7; postorbital, 8 to 9.5; distance from snout to dorsal fin, 55 to 61; snout to pelvic fin, 43 to 46.5; isthmus to pelvic fin, 30 to 32.5; anus to pelvic fin, 14.5 to 18; anus to base of caudal, 39 to 41.5; length of first dorsal when depressed, 6 to 7.7; distance between origins of dorsal fins, 12.5 to 17; base of second dorsal, 8 to 11.5; height of second dorsal, 7.8 to 10; base of anal, 17.5 to 21.6; length of pec-

TABLE V.—MEASUREMENTS AND COUNTS OF INTERGRADES BETWEEN *A. a. affinis* AND *A. a. littoralis*

	Morro Bay			Surf			Mouth of San Luis Creek						
Length to base caudal, mm.....	148	135	115	135	128	126	166	166	156	146	156	132	101
Length of head in length to base of caudal	4.9	4.85	4.45	4.75	4.8	4.8	5.0	5.0	5.0	4.9	4.9	4.7	4.8
Length of eye in hundredths of length to base of caudal.....	5.5	5.4	6.0	5.6	5.6	5.6	5.5	4.8	5.5	5.6	5.7	6.0	6.0
Interorbital width in head.....	3.5	3.2	3.35	3.2	3.5	3.1	3.2	3.35	3.2	3.35	3.25	3.1	3.5
Depth of caudal peduncle in head.....	2.9	2.7	3.0	2.8	2.8	2.7	2.6	2.7	2.7	2.8	2.7	2.7	3.1
Length of head in distance from isthmus to anus.....	2.3	2.35	2.0	2.2	2.25	2.2	2.35	2.3	2.35	2.25	2.1	2.3	2.2
Length of pectoral fin.....	21.5	20.3	20.7	22.5	22	21	19	21	22	18	21	18	...
Transverse scale-rows.....	64	68	61	57	62	61	56	64	63	57	63	59	61

toral fin, 17.8 to 22; length of pelvic, 8.5 to 10.5. Number of spines in first dorsal, 5 to 7; soft rays in second dorsal, 9 to 13; soft rays in anal, 18 to 23; pectoral rays, 13 to 15; number of transverse scale-rows, 56 to 64.

The following table gives typical examples of the combining, in single specimens of these intergrades, of the contrasted characters of both *A. a. affinis* and *A. a. littoralis*. The measurements and scale counts printed with bold-faced type are typical of, or most like, those of *affinis*, while the measurements and scale counts in light-faced type are like those characteristic of *littoralis*.

2b.—*A. affinis littoralis* varying toward *A. affinis affinis*

Atherinops affinis JORDAN AND GILBERT, 1880, Proc. U. S. Nat. Mus., III, (1881), p. 456 (Santa Barbara). JORDAN AND JOUY, 1881, idem, IV, p. 13 (Santa Barbara). EIGENMANN AND EIGENMANN, 1892, Ann. N. Y. Acad. Sci., VI, p. 352 (Santa Barbara). GILBERT, 1893, Rept. U. S. Fish Comm., (1896), p. 465 (Santa Barbara).

Range.—Mainland shore of the Santa Barbara Channel, southern California.

Record-stations.—Near Goleta: in channel forming outlet and inlet of estero; abundant; breeding; July 5. Santa Barbara: recorded by Jordan and Gilbert, and others, as *A. affinis*. Near Carpenteria: abundant in the muddy water of El Estero; breeding; July 4.

Relationships.—This race of *Atherinops*, while fairly typical of *littoralis*, shows a definite approach toward *affinis* in the size of the scales (see Table II, p. 414) and in other characters indicated below. As in the case of the last race, those items, in which each specimen listed in the following table resembles typical *affinis*, are emphasized by bold-faced type.

TABLE VI.—MEASUREMENTS AND COUNTS OF SPECIMENS OF *A. a. littoralis*
VARYING TOWARD *A. a. affinis*

	Near Goleta			Santa Barbara	El Estero, near Carpenteria			
Length to base caudal, mm.....	110	101	94	115	137	113	123	120
Length of head in length to base of caudal	4.3	4.65	4.5	4.4	4.65	4.8	4.6	4.5
Length of eye in hundredths of length to caudal base.....	7.3	6.3	6.6	6.2	6.3	6.3	6.3	6.2
Interorbital width in head.....	3.5	3.2	2.9	3.6	3.4	3.45	3.4	3.35
Depth of caudal peduncle in head.....	3.0	2.8	2.7	2.95	3.1	3.0	2.85	2.8
Length of head in distance from isthmus to anus.....	1.9	2.0	1.9	2.2	2.3	2.1	2.2	2.3
Length of pectoral fin.....	22.7	21	21.5	21	21.5	20	19.5	21.5
Transverse scale-rows.....	57	64	61	57	58	58	55	57

3.—*Atherinops affinis littoralis*, new subspecies

Atherinops affinis STEINDACHNER, 1875, Sitzb. Akad. Wiss. Wien, LXXII, p. 89 (San Diego record). JORDAN AND GILBERT, 1880, Proc. U. S. Nat. Mus., III, p. 29 (San Diego). ROSA SMITH, 1880, A List of the Fishes of San Diego (San Diego). JORDAN AND GILBERT, 1880, Proc. U. S. Nat. Mus., III, (1881), p. 456 (San Pedro; San Diego). JORDAN AND JOUY, 1881, idem, IV, p. 13 (Wilmington). JORDAN AND GILBERT, idem, p. 43 (in part; "Cape Mendocino southward"); 1883, Bull. U. S. Nat. Mus., XVI, p. 409 (in part; "Pacific Coast"). GILBERT, 1891, Proc. U. S. Nat. Mus., XIV, p. 549 (locality not given; probably San Diego). EIGENMANN, 1891, Amer. Nat., XXV, p. 579 (San Diego); 1892, Proc. U. S. Nat. Mus., XV, pp. 129, 146 (San Diego). EIGENMANN AND EIGENMANN, 1892, Ann. N. Y. Acad. Sci., VI, p. 352 (San Diego; San Pedro). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807 (in part; "Coast of California"). STARKS AND MORRIS, 1907, Univ. Cal. Publ. Zool., III, p. 187 (in part; "San Francisco to Magdalena Bay"). METZ, 1912, Ann. Rept. Laguna Mar. Lab. (Pomona College), I, p. 31 (Newport Bay; Laguna Beach). JORDAN AND SNYDER, 1913, Proc. U. S. Nat. Mus., XLV, p. 576 (locality not given; probably San Diego).

Range.—Mainland shores of Ventura, Orange, Los Angeles, and San Diego Counties, in southern California; probably of northern Lower California also, although there are no records from that region.

Record-stations.—Ventura: in brackish water lagoon at mouth of Ventura River. Redondo: abundant about sewer outlet under wharf; a partially protected beach. San Pedro Bay: recorded by Jordan and Gilbert and others as *A. affinis*. Alamitos Bay, Orange County: specimens obtained in sloughs (a mature female 95 mm. long to caudal collected on Juen 6, when no young were observed; many of both sexes, the longest 102 mm. long, seined on August 6, on which date young about an inch long were especially abundant). Sunset Beach: specimens caught from wharf, near surf, on August 6. Newport Bay and Laguna Beach: recorded by Metz as abundant throughout the summer. Near Del Mar: young taken in salt water lagoon just north of town. La Jolla: specimens in the Scripps Institution for Biological Research, collected on April 18. Mission Bay (False Bay): specimens taken near mouth of bay. Point Loma: numerous young specimens, from 43 to 61 mm. long without caudal, collected on December 31, in a rocky tide-pool on the ocean side of the Point; schools of half-grown individuals noted in the summer just off the same rocks. San Diego Bay: recorded by authors in general, as *A. affinis*; common throughout the year, congregating in especial abundance about the sewer outlet; breeding in spring and early summer (May and June, according to Eigenmann; one of the type lot, taken April 2, has matured ova); larvæ recorded by Eigenmann as abundant in the bay.

Habits.—In addition to the notes just given, a few other details of the habits of *littoralis* may be added: like *Mugil*, it feeds largely on mud, with which the alimentary canal is often distended; it swims in rather large groups near the surface; it tolerates both muddy and clear water; it seems to remain close inshore everywhere and may be taken in abundance in seines. Like the other species of the genus, all of which have been examined in this respect, *littoralis* breeds first at the age of two years; the larger adults are three or four years old. The age-determinations upon which these conclusions are based were made on several specimens of each of the several forms in the genus. The seasonal marks, checks, or annuli, on the scales, supposedly formed during the winter, are well developed in *Atherinops*. The first annulus is often indistinct and sometimes is not apparent in the first year group among schools of fishes taken at the beginning of the breeding season.

Atherinops affinis littoralis is a food fish of good quality, though rather bony. It is usually found in the markets, being known, along with *Atherinopsis californiensis*, as "Smelt." The fishermen, it is true, frequently distinguish it from that species under the name of "Top-smelt," or "Little Smelt" (in allusion to its swimming habits or its small size), while they refer to the larger species as the "Jack-smelt" or "Blue-smelt."¹

Nomenclature.—*Atherinops affinis littoralis* is well differentiated from *A. a. affinis*, but is regarded as a subspecies because of the intergradation of the two forms. The fact that the intergradation is interpreted as probably the result of the thorough hybridization of two formerly distinct species can not alter the situation from a nomenclatural point of view, because of the difficulties surrounding the general application or testing of such an interpretation.

Despite the obvious nature of the differences which distinguish the two, *littoralis* has not previously been separated from *affinis*; they have probably never been directly compared. The types of *insularum* and *oregonia* were contrasted with specimens of *littoralis* on the erroneous assumption that the latter were typical of *affinis*.

Holotype.—A female with ripening ova, 143 mm. long to caudal base; Cat. No. 2064, Field Museum of Natural History; collected by the Bureau of Fisheries' Steamer *Albatross*, at North Island, San Diego Bay, California, April 2, 1894.

Description and Comparisons.—*A. a. littoralis* is a more trimly built fish than *A. a. affinis*: the dorsal contour is not elevated at the occiput, as it is in that form, and the caudal peduncle is decidedly more slender (Table

¹ These fishes are known to the Latin fishermen chiefly as Pescado del Rey, or similar names signifying "Fish of the King."

III, p. 415). The tip of the premaxillaries are on a level with the middle of the pupil, instead of its lower border. The head is relatively longer (Tables XIII and XIV) but proportionately narrower (Table XV). The larger comparative size of the eye (Table XVII) is accentuated by the lesser development of adipose tissue about it. The paired fins are longer, the difference in the case of the pectoral being noteworthy (Table XIX); the first dorsal is also, on the average, a little higher, its length, when depressed, being constantly less than half the distance between the two dorsals (Table XVIII). The scales (Table II) in *littoralis* are constantly larger than in *affinis*, and they seem to be more regularly arranged anteriorly. The smaller size of *littoralis* (Table VIII) and its general darker tone of color serve further to distinguish it from *affinis*. Otherwise, the two forms are apparently similar.

A. a. littoralis differs from the three island forms of *Atherinops* in various characters, as outlined in the comparative tables referred to above. It is distinguished from all by the greater compression of the body and by the larger size of the scales. When compared with these island forms, *littoralis* is found to resemble *insularum*, of the adjacent islands, the least. It differs from that form in the following characters: scales larger; dorsal spines on the average more numerous; pectoral fin longer; first dorsal higher; head narrower and comparatively longer; snout shorter; eye longer; body more robust; size smaller.

Measurements and Counts of the holotype, supplemented by those of eleven paratypes from San Diego Bay, Alamitos Bay, and Ventura.—Length to base of caudal, 143 mm. (91 to 148 mm.); length of head into length of body to caudal, 4.6 (4.2 to 4.85); depth of body, 4.75 (4.15 to 5.15); least depth of caudal peduncle into length of head, 2.83 (2.8 to 3.15); length of snout, 3.4 (3.35 to 3.85); least interorbital width, 3.35 (3.35 to 3.8); postorbital length of head, 2.25 (2.2 to 2.45); length of head into distance from isthmus to anus, 2.05 (2.0 to 2.3). Measurements in hundredths of length to caudal base: length of head, 21.5 (20.5 to 23.3); depth of body, 21 (20 to 23.3); depth of caudal peduncle, 8 (7.5 to 8); length of snout, 6.5 (5.7 to 7); length of upper jaw, 6.5 (6 to 7); diameter of eye, 6.3 (5.7 to 7); interorbital width, 6.6 (6 to 7); length of postorbital, 10 (9 to 10.2); distance from snout to dorsal fin, 61.5 (58 to 62); snout to pelvic fin, 43.3 (43 to 47.5); isthmus to pelvic fin, 27.5 (28 to 32.5); anus to pelvic fin, 17.3 (14.5 to 17); anus to base of caudal, 40.5 (40 to 43.5); length of first dorsal when depressed, 8 (6.7 to 8.2); distance between origins of dorsal fins, 12.8 (11.2 to 14.3); base of second dorsal, 8.7 (8 to 10); height of second dorsal, — (9 to 10.5); base of anal, 19.7 (18 to 21.5); distance between bases of anal and caudal fins (length of caudal peduncle), 17.5 (16.5 to 19); length of

lower caudal lobe, — (21.5 to 26.5); length of pectoral fin, 22 (21.7 to 24.8); length of pelvic fin, 10.7 (10 to 11). Number of spines in first dorsal fin, 7 (5 to 7); number of soft rays in second dorsal, 10 (8 to 11); soft rays in anal, 22 (17 to 24); pectoral rays, 14 (13 or 14); number of transverse scale-rows, 56 (53 to 58).

3a.—Intergrades between *A. affinis littoralis* and *A. affinis magdalenæ*.

Atherinops affinis OSBURN AND NICHOLS, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 156 (Port San Bartolomé).

Range.—Mainland shore on the ocean side of central Lower California.

Record-station.—Port San Bartolomé, San Bartolomé Bay, central Lower California; specimens seined on March 13, the smallest 32 mm. long to caudal; others taken April 23.

Comparisons.—These intergrades have been discussed in some detail in a former connection (see p. 415). Further comparison between them and *littoralis* on the one hand, and *magdalenæ* on the other, is made in the comparative tables (II, p. 414; III, p. 415; VIII–XIX, pp. 437–440).

Measurements and Counts of eight specimens from Port San Bartolomé.—Length to base of caudal, 107 to 124 mm.; length of head into total length to base of caudal, 4.35 to 4.65; depth of body, 4.5 to 5.2; least depth of caudal peduncle in length of head, 2.6 to 2.9; snout, 3.4 to 3.7; upper jaw, 3.4 to 3.7; eye, 3.35 to 3.7; interorbital, 3.2 to 3.4; postorbital, 2.35 to 2.4; length of head into distance from isthmus to anus, 1.9 to 2.2. Measurements in hundredths of length to base of caudal fin: head, 21.5 to 23; depth of body, 20 to 22; depth of caudal peduncle, 7 to 8.5; snout, 6 to 7.5; upper jaw, 6 to 7.5; eye, 6 to 7.3; interorbital, 6.5 to 7.3; postorbital, 9 to 9.7; snout to dorsal, 59 to 62; snout to pelvic, 44 to 48; isthmus to pelvic, 28 to 32; anus to pelvic, 14.5 to 17; anus to base of caudal, 41 to 44; length of first dorsal when depressed, 7 to 8.2; distance between origins of dorsals, 11.4 to 13.3; base of second dorsal, 8.5 to 10.5; height of second dorsal, 9.2 to 10.3; base of anal, 21.5 to 23; length of pectoral, 21.5 to 24; length of pelvic, 10 to 11. Number of spines in first dorsal fin, 5 or 6; soft rays of second dorsal, 9 or 10; soft rays of anal, 20 or 21; pectoral rays, 13 to 15; number of transverse scale-rows, 55 to 58.

4.—*Atherinops affinis magdalenæ* Fowler

?*Atherinopsis californiensis* LOCKINGTON, 1881, Proc. Acad. Nat. Sci. Phila., p. 114 (? based upon the specimens subsequently serving as the types of *Atherinops magdalenæ*); (Magdalena Bay).

Atherinops magdalenæ FOWLER, 1903, idem, (1904), p. 740, Pl. xlii (Magdalena Bay).

Atherinops affinis STARKS AND MORRIS (after Gilbert MS.), 1907, Univ. Cal. Publ. Zool., III, p. 187 (Magdalena Bay). OSBURN AND NICHOLS, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 156 (Magdalena Bay; Santa Maria Bay).

Range.—Southwestern Lower California.

Record-stations.—Magdalena Bay; Santa Maria Bay. The material reported on here has already been recorded by Starks and Morris, and by Osburn and Nichols. The material of the latter lot was collected by the 1911 expedition of the *Albatross*: on March 18, at Santa Maria Bay; on March 20, on the beach on the outer side of Mangrove Island, Magdalena Bay¹; and on March 21, off Magdalena.

Habits.—Nothing definite concerning the habits of *magdalenæ* has been published. Judging from the size of the series collected by the *Albatross* on two occasions, the species is probably common in Magdalena Bay. In addition to remains of algæ, small gastropod shells and shell fragments were found in the stomachs of large specimens.

Comparisons.—*A. a. magdalenæ* is much more closely related to *A. a. littoralis* than to any other form of the genus. It differs from *littoralis*, and resembles *affinis*, however, in its deeper caudal peduncle, and further approaches *affinis* in its larger size, somewhat smaller eye, and paler coloration. It differs from *affinis* and resembles *littoralis* in the following characters: the dorsal contour is not elevated at the occiput; the tip of the premaxillaries are on a level with the middle of the pupil, rather than its lower border; the head is relatively longer; the interorbital, narrower; the eye, larger; the paired fins, longer; the scales, larger (see comparative tables).

As in related forms, the position of the spinous dorsal is variable, being either over or behind the anus; hence this character, used in the distinction of *magdalenæ* from *affinis* by Fowler, proves to be of little systematic value. The number of transverse scale-rows (52 to 58) is higher in the material examined than that given for the type (47). The peritoneum is not silvery gray as originally described, but black, as in all other species of *Atherinops*.

Measurements and Counts of fourteen topotypes of *Atherinops affinis magdalenæ*.—Length to caudal base, 93 to 172.5 mm.; head in total length to caudal, 4.1 to 4.88; depth of body, 4.88 to 5.17; least depth of caudal peduncle in head, 2.4 to 2.7; snout, 3.45 to 3.6; upper jaw, 3.3 to 3.7; eye, 3.5 to 4.1; interorbital, 3.3 to 3.6; postorbital, 2.2 to 2.35; length of head in distance from isthmus to anus, 1.9 to 2.15. Measurements in hundredths of length to base of caudal fin: head, 21 to 22.7; depth of body, 20 to 21, depth of caudal peduncle, 8.2 to 8.6; snout, 6.2 to 6.7; upper jaw, 6 to 7;

¹ See Townsend, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 417.

eye, 5.5 to 6.5; interorbital, 6.5 to 7; postorbital, 9 to 10.3; distance from snout to dorsal fin, 59 to 62; snout to pelvic fin, 43 to 48; isthmus to pelvic fin, 26.5 to 30.5; anus to pelvic fin, 14 to 16; anus to base of caudal, 42 to 42.5; length of first dorsal when depressed, 7 to 8; distance between origins of dorsal fins, 10.8 to 15.5; base of second dorsal, 10.5 to 11; height of second dorsal, 9.5 to 10.5; base of anal fin, 21 to 22; length of caudal peduncle (base of caudal to end of anal base), 15.5 to 18; length of pectoral fin, 21 to 22.6; length of pelvic fin, 10.2 to 11.5. Number of spines in first dorsal fin, 5 to 7; soft rays of second dorsal, 9 to 12; soft rays of anal, 20 or 21; pectoral rays, 13 or 14; number of transverse scale-rows, 52 to 58.

Atherinops insularum Gilbert

Although the relations of the three island forms of *Atherinops* have already received some attention (pp. 410 to 412), a general comparison between them and three mainland forms of the subgenus may precede the more detailed discussion of each form.

The island races of *Atherinops* are all trimly built fishes, resembling *Atherinopsis californiensis* in form; they are less compressed and usually less robust than the mainland races. In addition to their form, the island races, considered together, differ from those of the mainland in only one character: the pectoral rays on the average are more numerous; in both cases the mode of variation is at fourteen rays, but along the mainland the pectoral fin contains thirteen rays more frequently than fifteen, whereas on the islands the reverse is true:

<i>Pectoral rays</i>	13	14	15	16
Mainland (75 specimens)	17	54	4	—
Islands (55 specimens)	1	31	22	1

The island forms of *Atherinops*, as previously discussed, probably are related to *A. a. affinis* of the northern mainland more closely than to *A. a. littoralis* and to *A. a. magdalenæ*: they resemble *affinis* in the small size of the scales (Table I, p. 411); in the width of the head (Table XV, p. 439), and in the shortness of the pectoral (Table XIX). The size of the scales is the most clearly diagnostic among these characters; the width of the interorbital in *cedroscensis* is no greater than that of the intergrades between *littoralis* and *magdalenæ*, which inhabit the adjacent main-shore, although wider than in typical specimens of any of the mainland forms; the pectorals are not much shorter in *guadalupæ* than in *magdalenæ*. The island forms, as a whole, differ from *affinis* proper in the more slender form, particularly of the caudal peduncle (see Table IX, p. 437); in the slightly higher position of the mouth, the tip of the premaxillaries being on a level with the middle

rather than the lower edge of the pupil; and in the greater length of the head as compared with the distance from isthmus to anus. In addition to these general differences, each of the island forms may be distinguished by several characters from each of the mainland forms, considered separately.

Some zoologists would not apply trinominal nomenclature to these island forms, as obviously no actual intergradation can occur between them. Two of the forms, *insularum* and *guadalupæ*, are surely sufficiently differentiated to be contrasted as distinct species, if they alone were known. But *cedroscensis* is intermediate between the other two: the range of its variation overlaps that of both *insularum* and *guadalupæ* in the case of each of the contrasted characters, except the interorbital width. Consequently the relationships of the three forms seem to be well expressed by the use of trinominal names. Those ichthyologists who demand a strict demonstration of intergradation for the recognition of forms as subspecies may use binominal nomenclature in this case.

5.—*Atherinops insularum insularum* Gilbert

Atherinops insularum GILBERT, 1891, Proc. U. S. Nat. Mus., XIV, p. 549 (in part; San Clemente Is.; San Nicholas Is.). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807 (after Gilbert). STARKS AND MORRIS, 1907, Univ. Cal. Publ. Zool., III, p. 187 (in part; Santa Cruz Is.; San Nicholas Is.; San Clemente Is.). JORDAN AND SNYDER, 1913, Proc. U. S. Nat. Mus., XLV, p. 576 (the particular island not mentioned).

Atherinops affinis GILBERT, 1898, Rept. U. S. Fish Comm. (1899), p. 25 (Santa Catalina Island).

Range.—Shores of the Santa Barbara (or Channel) Islands, off southern California.

Record-stations.—Santa Cruz Island; recorded by Starks and Morris, after Gilbert, MS. San Nicholas Island: Gilbert. Santa Catalina Island: recorded by Gilbert, as *A. affinis*; two specimens examined from near Avalon, received from the Los Angeles High School. San Clemente Island: Gilbert. Specimens were examined from each of these islands except Santa Cruz.

Habits.—Nothing definite is known concerning the habits of *insularum*. The form of the fish would indicate that it is a stronger swimmer than the mainland species, a characteristic probably correlated with the absence of estuaries about the islands.

Comparisons.—*A. i. insularum* differs from *A. a. littoralis*, and approaches, resembles, or exceeds in its variations, *A. a. affinis* of the mainland farther north, in the following characters: scales smaller; head broader and shorter; fins shorter; eye smaller; size larger (see comparative tables at end of the paper). It differs from both *littoralis* and *affinis* in its longer, sharper snout,

and in its more nearly terete body, in which respects it resembles *Atherinopsis californiensis*, and further, on the average, in the fewer dorsal spines and more numerous pectoral rays.

TABLE VII.—MEASUREMENTS AND COUNTS OF *Atherinops insularum insularum*

	San Clemente	San Nicholas	Santa Catalina
Number of specimens.....	4	4	2
Length to base of caudal, mm.....	100 to 155	147 to 220	120, 135
Head in total length to caudal.....	4.6 to 5.2	4.9 to 5.4	4.7, 4.7
Depth of body.....	5.4 to 5.8	4.9 to 5.6	5.35, 5.4
Depth of caudal peduncle in head...	2.9 to 3.3	2.7 to 3.0	3.0, 3.05
Length of snout.....	3.15 to 3.35	3.15 to 3.4	3.3, 3.35
Length of upper jaw.....	3.2 to 3.6	3.5 to 3.7	3.4, 3.6
Diameter of eye.....	3.6 to 4.0	4.2 to 4.33	4.0, 4.1
Width of interorbital.....	3.05 to 3.25	3.0 to 3.15	3.2, 3.2
Length of postorbital.....	2.25 to 2.4	2.15 to 2.2	2.2, 2.3
Length of head in distance from isthmus to anus.....	1.9 to 2.1	2.25 to 2.4	2.2, 2.3
<i>Measurements in hundredths of length to caudal base</i>			
Length of head.....	20.5 to 22	19.5 to 20.5	21, 22
Depth of body.....	17 to 19	18.8 to 20.3	18.6, 19
Depth of caudal peduncle.....	6.7 to 7.8	7 to 7.6	7.3, 7.5
Length of snout.....	6.2 to 7.2	5.7 to 6.5	6.7, 6.7
Length of upper jaw.....	6 to 7.2	5.4 to 6	6.3, 6.6
Diameter of eye.....	5.4 to 6	4.6 to 4.8	5.6, 5.6
Width of interorbital.....	6.5 to 7.2	6.5 to 6.7	7, 7
Length of postorbital.....	8.8 to 9	8.8 to 9.7	9.6, 9.7
Distance, snout to dorsal fin.....	55.7 to 58.2	54 to 57.2	57, 59
“ snout to pelvic fin.....	42.3 to 43.5	42.3 to 45	45, 46
“ isthmus to pelvic fin.....	27.5 to 28.8	28.7 to 32	30, 32
“ anus to pelvic fin.....	13 to 14.8	14.6 to 16.3	15.5, 16
“ anus to base of caudal.....	44 to 45.3	41.5 to 44	41, 43.3
Length of first dorsal when depressed	6 to 6.3	5.6 to 6.4	6, 6.4
Distance between origins of dorsal fins	12.6 to 15.2	13.2 to 17	12.7, 13.4
Base of second dorsal fin.....	10.2 to 11.8	9.6 to 11	9.5, 10.4
Height of second dorsal fin.....		10	9
Base of anal fin.....	23 to 24	22 to 23.7	20.5, 22.5
Length of caudal peduncle.....	16.8 to 18.8	16.6 to 18.5	17, 18.4
Length of pectoral fin.....	19 to 20.3	18.6 to 20.7	20.3, 20.4
Number of rays: first dorsal.....	V or VI	V	V, VI
“ “ “ second dorsal.....	I, 10 or I, 11	I, 10	I, 9, I, 11
“ “ “ pectoral.....	14 or 15	14	15, 15
“ “ “ anal.....	I, 21 to I, 23	I, 20 or I, 21	I, 20, I, 22
Number of transverse scale-rows....	66 to 72	65 to 70	63, 65

6.—*Atherinops insularum cedroscensis*, new subspecies

Atherinops affinis STARKS AND MORRIS (after Gilbert MS.), 1907, Univ. Cal. Publ. Zool., III, p. 187 (in part; Cedros Island).

Atherinops insularum OSBURN AND NICHOLS, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 156 (Cedros Is.; San Benito Is.).

Range.—Cedros and San Benito Islands, off the coast of central Lower California.

Record-stations.—Cedros Island (also known as Cerros Is.): Starks and Morris, after Gilbert MS, as *Atherinops affinis*; southeast side of island, March 11, 1911 (Osburn and Nichols, as *A. insularum*). West San Benito Island: young specimens, the largest 67 mm. long to caudal, collected March 9, 1911, and recorded by Osburn and Nichols as *A. insularum*. All of the known specimens were collected by the naturalists of the United States Bureau of Fisheries' Steamer *Albatross*, and all have been re-examined.

Atherinops insularum cedroscensis resembles closely both *A. i. guadalupæ* and *insularum* in those respects in which those two forms agree with each other, with the single exception that its head is slightly narrower. In those characters by which *guadalupæ* differs from *insularum*, *cedroscensis* is intermediate, the range of its variation in the case of each distinctive feature overlapping that of the two related forms (see comparative tables at the end of this paper).

Habits.—The Cedros Island *Atherinops* was collected on the southeast and east sides of that island on March 11, 1911, and reported to be of "excellent quality and very abundant."¹ Two specimens obtained at Cedros Island, by the *Albatross* on a former occasion, had their stomachs distended by small crustacea, the one 116 mm. long to caudal containing in addition a myctophid fish 13.5 mm. long.

Nomenclature.—*A. i. cedroscensis* has been recorded under the names of *affinis* and *insularum*, its distinctive features not having been appreciated.

Holotype.—A female specimen with ripening ova, 175 mm. long to caudal (Cat. No. 7144, American Museum of Natural History); collected by the *Albatross* on the southeast side of Cedros Island, off the coast of central Lower California, on March 11, 1911.

Comparisons.—*Atherinops insularum cedroscensis*, like the other island forms, has a gracefully slender and not strongly compressed body; the dorsal contour is scarcely elevated at the occiput; the caudal peduncle is slender. The head is of moderate length, and apparently somewhat narrower than in the other island races. The eye is larger than in *affinis* or

¹ Townsend, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 410, fig. 8.

insularum, being a little shorter than the snout, which is less produced than in *insularum*. The tip of the premaxillaries are on a level with the middle of the pupil; the forked teeth are arranged in a single series on each jaw.

Measurements and Counts of the type of *cedroscensis*, supplemented by those of ten paratypes.—Length to base of caudal fin, 175 mm. (110 to 166 mm.); length of head in total length to caudal, 5.15 (4.5 to 4.9); depth of body, 5.0 (4.6 to 5.5); depth of caudal peduncle into head, 3.0 (2.9 to 3.05); length of snout, 3.5 (3.25 to 3.6); length of upper jaw, 3.6 (3.4 to 3.7); diameter of eye, 3.8 (3.4 to 4.0); width of interorbital, 3.2 (3.2 to 3.4); length of postorbital, 2.15 (2.2 to 2.5); length of head in distance from isthmus to anus, 2.25 (1.9 to 2.35). Measurements in hundredths of length to base of caudal: head, 20.2 (20.7 to 22.2); depth of body, 20.4 (17.5 to 21.5); depth of caudal peduncle, 6.8 (7 to 7.8); distance from snout to origin of dorsal fin, 58.5 (56 to 59); snout to pelvic fin, 46 (43.5 to 46); isthmus to pelvic fin, 31 (27 to 31); anus to pelvic fin, 15 (14 to 16); anus to base of caudal, 41.8 (41 to 43); length of first dorsal fin when depressed,—(6 to 8); distance between origins of dorsal fins, 14 (13.5 to 15.5); base of second dorsal, 10.5 (9.6 to 11); height of second dorsal,—(7.5 to 9); base of anal fin, 22.5 (20.5 to 22.5); length of pectoral fin, 20 (19 to 21.6); length of pelvic fin, — (9 to 10). Number of spines in first dorsal fin, 6 (5 to 7); soft rays in second dorsal, 11 (10 or 11); pectoral rays, 14 (14 or 15); soft rays in anal fin, 24 (18 to 23); number of transverse scale-rows, 63 (61 to 70).

7.—*Atherinops insularum guadalupæ*, new subspecies

Atherinops insularum GILBERT, 1891, Proc. U. S. Nat. Mus., XIV, p. 549 (in part; Guadalupe Island). JORDAN AND EVERMANN, 1898, Bull. U. S. Nat. Mus., XLVII, part 2, p. 807 (in part; after Gilbert). STARKS AND MORRIS, 1907, Univ. Cal. Publ. Zool., III, p. 187 (in part; after Gilbert). OSBURN AND NICHOLS, 1916, Bull. Amer. Mus. Nat. Hist., XXXV, p. 156 (in part; Guadalupe Is.).

Range and Record-station.—Guadalupe Island, off Lower California (see Map, opposite p. 412); first obtained by the *Albatross* on February 28, 1889, and recorded by Dr. Gilbert as *Atherinops insularum*, in the type description of that form; again collected by the *Albatross*, with the use of dynamite, on March 2, 1911, and recorded by Osburn and Nichols as *A. insularum*.

Habits.—Almost wholly unknown. It seems to spawn earlier, and perhaps longer, than the mainland forms, a female 147 mm. long to caudal (Cat. No. 46667, U. S. N. M.), taken February 28, being mature, while another of the same length (the type specimen), taken March 2, has ripening ova.

Nomenclature.—Recorded twice as *Atherinops insularum*, this form has remained without a distinctive name.

Holotype.—A female with ripening ova, 147 mm. long to base of caudal fin; collected by the *Albatross* with the use of dynamite, at Guadalupe Island, March 2, 1911; Cat. No. 7145, American Museum of Natural History.

Comparisons.—The Guadalupe Island *Atherinops* differs widely and unmistakably from *A. i. insularum* of the Santa Barbara Islands, although it resembles that form more closely than it does any of those occurring on the mainland. The body is subterete, being usually more slender than *insularum*, and decidedly more slender and less compressed than the mainland forms; the caudal peduncle is even more slender than in *insularum*. The head averages longer and broader than in any other form of the subgenus; the eye is large, averaging slightly larger than in *littoralis*, and being much larger than in *affinis* or *insularum*; the snout is blunter and usually less pointed than in *insularum*. The position and form of the mouth is like that of *littoralis* and *insularum*; the teeth are bifid like those of the other forms of the subgenus. The first dorsal fin is higher than in *insularum*, extending, when depressed, more than half way to the origin of the second dorsal; the spines are more frequently six than five, while the reverse is true for *insularum*; the pectoral rays average slightly more than in the mainland forms; in its length the pectoral fin of *guadalupæ* is intermediate between that of *A. i. insularum* on the one hand, and that of *affinis* or *littoralis* on the other. The Guadalupe subspecies has the scales as small as those of *affinis*, but on the average not so numerous as in *insularum* (see Table I, p. 411). The color is darker than in *affinis* or *magdalenæ*; the size attained seems to be somewhat less than in the case of *affinis* or *insularum*. The measurements and counts serving as the basis for these comparisons are given below; the comparisons are repeated in more graphic form in the following tables.

Measurements and Counts of the type of *A. i. guadalupæ*, supplemented by those of fifteen paratypes.—Length to base of caudal, 147 mm. (123 to 147 mm.); length of head in total length to caudal, 4.4 (4.2 to 4.8); depth of body, 5.2 (5.15 to 5.5); depth of caudal peduncle in length of head, 3.35 (3.1 to 3.4); length of snout in head, 3.35 (3.2 to 3.6); length of upper jaw, 3.5 (3.35 to 3.8); diameter of eye, 3.6 (3.2 to 3.6); width of interorbital, 2.95 (2.9 to 3.15); length of postorbital, 2.35 (2.2 to 2.4); length of head in distance from isthmus to anus, 1.85 (1.75 to 2.1). Measurements in hundredths of length to caudal base: length of head, 23 (21 to 24); depth of body, 19.5 (18 to 20); least depth of caudal peduncle, 7 (7 to 7.5); distance from snout to origin of first dorsal fin, 58 (54 to 57.5); snout to pelvic

fin, 43 (42 to 45); isthmus to pelvic fin, 27.5 (27 to 30); anus to pelvic fin, 15 (12.7 to 15); anus to base of caudal, 44 (42.5 to 45); length of first dorsal when depressed, — (7.3 to 8.8); distance between origins of dorsals, 13.3 (13.5 to 16.5); base of second dorsal, 9.5 (9 to 11.5); height of second dorsal, 10.5 (9 to 11); base of anal fin, 21.5 (21 to 23.5); length of pectoral fin, 21 (20 to 22); length of pelvic fin, 10.5 (9.8 to 11). Number of spines in first dorsal fin, 7 (5 to 7); soft rays in second dorsal, 10 (9 to 12); soft rays in anal,— (20 to 24); pectoral rays, 15 (14 or 15); number of transverse scale-rows, 65 (60 to 69).

V.— COMPARATIVE TABLES OF MEASUREMENTS AND COUNTS

In order to compare graphically the differential features of the six forms of the subgenus *Atherinops*, the following comparative tables have been prepared. They supplement those included in the preceding sections of the paper: size of the scales (Table I, p. 411; Table II, p. 414), and depth of the caudal peduncle (Table III, p. 415). The figures forming the basis of these comparative tables are generally given in the tables of measurements and counts for each form, but in certain cases additional figures are included.

TABLE VIII.— LENGTH TO CAUDAL BASE OF THE LARGEST SPECIMEN OF EACH FORM EXAMINED

<i>A. a. affinis</i>	227 mm.
Intergrades	163
<i>A. a. littoralis</i>	148
<i>A. a. magdalenæ</i>	172.5
<i>A. i. insularum</i>	220
<i>A. i. cedroscensis</i>	175
<i>A. i. guadalupæ</i>	147

TABLE IX.— DEPTH OF BODY (EXPRESSED IN HUNDREDTHS OF LENGTH TO CAUDAL BASE)

	17	18	19	20	21	22	23
<i>A. a. affinis</i>							
Intergrades							
<i>A. a. littoralis</i>							
Intergrades							
<i>A. a. magdalenæ</i>							
<i>A. i. insularum</i>							
<i>A. i. cedroscensis</i>							
<i>A. i. guadalupæ</i>							

TABLE X.—DEPTH OF CAUDAL PEDUNCLE (MEASURED INTO HEAD)

	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4
<i>A. a. affinis</i>												
Intergrades												
<i>A. a. littoralis</i>												
Intergrades												
<i>A. a. magdalenæ</i>												
<i>A. i. insularum</i>												
<i>A. i. cedroscensis</i>												
<i>A. i. guadalupæ</i>												

TABLE XI.—NUMBER OF SPINES IN THE FIRST DORSAL FIN ¹

	4	5	6	7
<i>A. a. affinis</i>	..	7	11	1
Intergrades	..	4	11	5
<i>A. a. littoralis</i>	1	6	10	4
Intergrades	..	2	3	..
<i>A. a. magdalenæ</i>	..	6	5	4
<i>A. i. insularum</i>	..	8	2	..
<i>A. i. cedroscensis</i>	..	4	6	1
<i>A. i. guadalupæ</i>	..	2	8	6

TABLE XII.—NUMBER OF PECTORAL RAYS ¹

	13	14	15	16
<i>A. a. affinis</i>	4	12	1	..
Intergrades	1	11	2	..
<i>A. a. littoralis</i>	4	9	..	..
Intergrades	1	5	1	..
<i>A. a. magdalenæ</i>	7	17	..	..
.....				
<i>A. i. insularum</i>	1	6	4	..
<i>A. i. cedroscensis</i>	..	16	11	1
<i>A. i. guadalupæ</i>	..	9	7	..

TABLE XIII.—LENGTH OF HEAD (MEASURED INTO LENGTH TO BASE OF CAUDAL)

	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7
<i>A. a. affinis</i>																
Intergrades																
<i>A. a. littoralis</i>																
Intergrades																
<i>A. a. magdalenæ</i>																
<i>A. i. insularum</i>																
<i>A. i. cedroscensis</i>																
<i>A. i. guadalupæ</i>																

¹ The number of individuals among those examined, having the given number of fin-rays, are listed in this table.

TABLE XIV.—LENGTH OF HEAD (MEASURED INTO DISTANCE FROM ISTHMUS TO ANUS)

[illegible]

TABLE XV.—LEAST INTERORBITAL WIDTH (MEASURED INTO HEAD)

	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5	3.6
<i>A. a. affinis</i>	.								
Intergrades									
<i>A. a. littoralis</i>									
Intergrades									
<i>A. a. magdalenæ</i>									
<i>A. i. insularum</i>									
<i>A. i. cedroscensis</i>									
<i>A. i. guadalupæ</i>									

TABLE XVI.—LENGTH OF SNOUT (MEASURED INTO HEAD)

	3.1	3.2	3.3	3.4	3.5	3.6	3.7	3.8	3.9
<i>A. a. affinis</i>									
Intergrades									
<i>A. a. littoralis</i>									
Intergrades									
<i>A. a. magdalenæ</i>									
<i>A. i. insularum</i>									
<i>A. i. cedroscensis</i>									
<i>A. i. guadalupæ</i>									

TABLE XVII.—LENGTH OF EYE (MEASURED INTO HEAD)

[illegible]

TABLE XVIII.—LENGTH OF DEPRESSED FIRST DORSAL FIN (MEASURED INTO SPACE BETWEEN ORIGINS OF DORSALS)

	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5	2.6	2.7	2.8	2.9	3.0
<i>A. a. affinis</i>																
Intergrades																
<i>A. a. littoralis</i>																
Intergrades																
<i>A. a. magdalenæ</i>																
<i>A. i. insularum</i>																
<i>A. i. cedroscensis</i>																
<i>A. i. guadalupæ</i>																

TABLE XIX.—LENGTH OF PECTORAL FIN (EXPRESSED IN HUNDREDTHS OF LENGTH TO BASE OF CAUDAL)

	17	18	19	20	21	22	23	24	25
<i>A. a. affinis</i>									
Intergrades									
<i>A. a. littoralis</i>									
Intergrades									
<i>A. a. magdalenæ</i>									
<i>A. i. insularum</i>									
<i>A. i. cedroscensis</i>									
<i>A. i. guadalupæ</i>									

Article XIV.—A SYNOPSIS OF THE NEARCTIC SPECIES OF THE GENUS *DROSOPHILA* (*SENSU LATO*)

BY A. H. STURTEVANT, COLUMBIA UNIVERSITY

This paper contains a tabulation of the Nearctic species of the genus *Drosophila*, as understood by the earlier authors. It includes those forms that will run to *Drosophila* by the keys given in Williston's 'Manual' (1908 edition). In addition to the Nearctic species, I have included four Neotropical species that are known to occur in southern Florida, so that the list is complete for the species known to me from the United States, Canada, and Alaska. All locality records for species are based on specimens that I have examined, unless they are placed in parentheses and followed by the name of the author concerned.

There are six genera in the group here under consideration, as follows:

1. Lower reclinate orbital large, situated nearer to upper reclinate than to proclinate; prescutellars well developed.....2.
Lower reclinate orbital nearer to proclinate than to upper reclinate; prescutellars usually not differentiated.....3.
2. Front thickly covered with stout hairs; costa reaches fourth vein.
Pseudophortica.
Front with at most a few fine hairs; costa very weak or absent beyond third vein.
Leucophenga.
3. Lower reclinate orbital large, placed below proclinate; postverticals usually small; eyes bare or nearly so.....*Chymomyza*.
Lower reclinate orbital usually small, placed above proclinate or, rarely, a trifle below it.....4.
4. One large pair of dorsocentrals; mesonotum and scutellum unusually convex above; shining black, marked with yellow.....*Mycodrosophila*.
Two large pairs of dorsocentrals (in our species).....5.
5. Acrostichal hairs in not more than four rows in front of anterior dorsocentrals, not more than two between the dorsocentrals.....*Scaptomyza*.
Acrostichal hairs in six or more rows in front, four or more behind..*Drosophila*.

PSEUDOPHORTICA Sturtevant, 1918, Jour. N. Y. Ent. Soc., XXVI, p. 37.

A single known species:

Three mm. long; yellowish. Va., Tenn., Fla., Ga., Ala., Tex.....*obesa* Loew.

LEUCOPHENGIA Mik, 1886, Wien. ent. Zeit., V, p. 317.

Recorded from the Palæarctic, Ethiopian, Oriental, and Neotropical regions. *Drosophila bellula* Bergroth (1894, Ent. Zeit. Stett., p. 45), from Queensland, Australia, evidently belongs here.

1. Palpi broad and flat; both crossveins and tips of first and second (sometimes also third) veins clouded. N. Y., Md., D. C., Ind., N. Car., Fla., Ala., Tex., Cuba, Hayti, Peru, (Pa., Ill., Kans.—Kahl).....*maculosa* Coquillett.
- Palpi clavate; tips of first and second veins with large dark spots. Mass., N. J., Pa., Md., D. C., Ind., Ill., Tenn., N. Car., Ga., Ala., La., (N. Y., W. Va., Kans.—Kahl).....*varia* Walker.

CHYMOMYZA Czerny, 1903, Zeits. Hymenopt., III, p. 199.

Recorded from the Palæarctic and Neotropical regions, and from the Seychelles.

1. Wings much spotted; front legs yellow. N. H., Vt., Mass., R. I., Conn., N. Y., N. J., Ind., Ill., Mo., Md., D. C., Va., N. Car., S. Car., Ala., Tex., (Pa.—Kahl; Mich., Kans.—Aldrich; Ga., La.—Melandar, *in litt.*)...*amæna* Loew.
- Wings clear, or blackish along anterior margin, or with a white tip; front femora, tibiæ, and first tarsal joints blackish.....2.
2. Front yellow or reddish yellow. N. H., N. Y., Ill., Va., Fla., Ala., Cuba, Trinidad, Panama, (Pa., Kans., Brazil — Kahl; St. Vincent — Williston).
-*procnemis* Williston.
- Front dark opaque brown.....3.
3. Wings clear; face whitish. Wash., (Hungary — Oldenberg).
-*caudatula* Oldenberg.
- Costal cell brown; face brown. Idaho.....*aldrichii* Sturtevant.

MYCODROSOPHILA Oldenberg, 1914, Arch. Naturgesch., LXXX, Abth. A, Heft 2, p. 4.

Recorded from the Palæarctic and Neotropical regions. *Drosophila gratiosa* de Meijere, from Java, and *D. fracticosta* Lamb, *D. nigerrima* Lamb, and *D. nigrobrunnea* Lamb, all three from the Seychelles, also belong here. There is a single Nearctic species:

- Two mm. long; found on fungi. N. H., Mass., N. J., Pa., Ind., Ill., Md., D. C., N. Car., Ga., Ala.....*dimidiata* Loew.

SCAPTOMYZA Hardy, 1849, Proc. Berwickshire Nat. Club, II, p. 361.

Recorded from the Palæarctic, Oriental, and Neotropical regions.

1. Four acrostichal rows in front of the suture; usually a spot at tip of third vein.....2.
- Two acrostichal rows in front; wings not spotted.....3.

2. Two large humeral bristles. Alaska, Wash., Idaho, Calif., Brit. Col., Colo., Quebec, Me., N. H., Mass., N. Y.....*terminalis* Loew.
One large humeral. N. H., Vt., Mass., N. Y., N. J., Ind., Ill., Kans., Colo., Md., D. C., Va., S. Car., Fla., Ala., La., Tex., (Bermuda — Johnson).
adusta Loew.
3. Dark brownish, pollinose on mesonotum; palpi yellow. Europe; N. H., Vt., Mass., N. Y., N. J., Md., D. C., Va., W. Va., Ind., Ill., S. Car., Ala., La., Tex., Kans., Idaho, Wash., Brit. Col.....*graminum* Fallén.
Yellowish, not pollinose; palpi dark. Fla., Cuba, Costa Rica, (Porto Rico — Coquillett).....*vittata* Coquillett.

DROSOPHILA Fallén, 1823, Dipt. Sveciæ Geomyzides, II, p. 4.

The genus comprises over 200 recognized species, occurring in practically all parts of the world, but especially common in tropical regions.

The "number of rows of acrostichal hairs" is to be counted just in front of the anterior pair of dorsocentral macrochætæ. The "costal index" is the number obtained by dividing the length of the second section of the costa by that of the third section; the "4th vein index" is obtained by dividing the length of the ultimate section of the fourth vein by that of the penultimate section; the "5x index" is obtained by dividing the length of the last section of the fifth vein by the length of the posterior cross-vein; the "4c index" is obtained by dividing the length of the third section of the costa by that of the penultimate section of the fourth vein.

1. Acrostichal hairs, just in front of anterior dorsocentral bristles, in six rows.....2.
Acrostichal hairs in eight rows.....20.
2. Facial carina very small, absent or very narrow below; second oral bristle not over half length of first.....3.
Carina broad below.....5.
3. Yellow; third antennal joint large, with long yellow hairs; fourth vein index under 2.0. Ill.....*duncani*, new species.
Blackish; third antennal joint as usual; fourth vein index over 2.0.....4.
4. Costal index 3.0 or over; a comb of stout black bristles on inner side of basitarsal joint of first leg of male. N. H., Mass., Conn., N. Y., N. J., Pa., Ind., Ill., Mo., Md., D. C., Va., N. Car., S. Car., Ga., Ala., Tex., Okla., Kans.
affinis Sturtevant.
Costal index under 2.5; no tarsal comb. Ala.....*alabamensis* Sturtevant.
5. Wings with about thirteen small dark spots along veins; mesonotum yellow, striped with reddish brown; first two to four oral bristles nearly equal. Mass., N. J., Ind., D. C., N. Car., Ala., Tex., (Fla.—Walker).
guttifera Walker.
Wings much clouded; posterior crossvein sinuate; small prescutellars present. N. Y., Ill., Md., D. C., Va., Tenn., N. Car., Ala., Tex.....*sigmoides* Loew.¹
Wings clear, or slightly clouded on crossveins or tips of longitudinal veins.....6.

¹ The species recorded as *D. sigmoides* by Ainslie (1906, Canad. Ent., XXXVIII, p. 44) from Minn. is really *D. inversa* Walker. I have examined the specimens in the U. S. National Museum.

6. A pair of presutural acrostichal bristles present; yellowish brown species. Frequents fungi. N. H., Vt., Mass., R. I., Conn., N. Y., N. J., Pa., Ill., Va., Tenn., N. Car., S. Car., Ga., Ala., Miss. *putrida* Sturtevant.
No presutural acrostichals. 7.
7. Second orbital about half length of first; only one large oral bristle; yellow species; $2\frac{3}{4}$ mm. long. N. H., Quebec. *ordinaria* Coquillett.¹
Second orbital less than half length of first. 8.
8. Costal index not more than 2.1. Neotropical species, found in southern Florida. 9.
Costal index not less than 2.5. 10.
9. Reddish brown species; bristles and branches of arista short. Lives in flowers. Fla., Cuba, Jamaica, Porto Rico, Costa Rica. *lutzii* Sturtevant.
Yellow; bristles and branches of arista as usual. Lives on fruit. Fla., Bahamas, Cuba, Jamaica, Hayti, Porto Rico, St. Vincent, Brit. Honduras, Costa Rica, Panama, Brazil. *willistoni* Sturtevant.
10. Ground color of mesonotum blackish or grayish, not at all yellowish. 11.
Ground color of mesonotum yellow, or reddish brown. 16.
11. Second oral bristle over half length of first; fourth vein index about 1.8. . . . 12.
Second oral less than half first. 13.
12. Carina broad; costal index about 3.0; $2\frac{3}{4}$ mm. long. N. Y. . . *virilis* Sturtevant.
Carina narrow; costal index about 4.0; $1\frac{1}{2}$ mm. long. Md., Va.
pseudomelanica Sturtevant.
13. Carina distinctly sulcate; mesonotum grayish pollinose, irregularly marked with reddish brown; about 3 mm. long. Ontario, N. H., Mass., Pa., Md., D. C., Va., Ga. *sulcata* Sturtevant.
Not as above. 14.
14. First coxæ black; $2\frac{1}{2}$ mm. long. See below, under 24, *robusta* Sturtevant.
First coxæ brown; 2 mm. long. 15.
15. Mesonotum blackish brown; "cheek" (from lower hind part of eye to lower hind corner of head) one-sixth greatest diameter of eye. N. H., Mass., R. I., N. Y., Md., Va., N. Car., Ga., Ala., Ind., Mo., Ark. *melanica* Sturtevant.
Mesonotum brownish black; "cheek" one-third diameter of eye. N. Car., Ga. Fla., Ala. *melanissima* Sturtevant.
16. Wings clear; abdomen banded; only one large oral bristle. Wash.
melanderi Sturtevant.
At least posterior crossvein slightly clouded. 17.
17. Reddish yellow; abdomen banded. Fla., Cuba, Hayti, Porto Rico, Dominica, Costa Rica, Panama. *cardini* Sturtevant.
Yellow, not reddish. 18.
18. Abdomen with interrupted dark posterior band on each of first four segments, and a median anterior spot on third, fourth and fifth segments. N. Y. (?), Ind., Md., Va., S. Car., Ala., La. *modesta* Sturtevant.
Abdomen spotted, but without median spots. 19.
- 19.² Dull yellow; tips of longitudinal veins not clouded. Europe, Me., N. H., Mass., N. Y., N. J., Md., Va., Tenn., Ind., Ill., Kans., Ala. *transversa* Fallén.

¹ *D. ordinaria* is listed in Smith's N. J. Catalogue. This is probably an error. All New Jersey specimens so labelled that I have seen are *D. transversa* Fallén or *D. putrida* Sturtevant.

² Study of living material and of spermathecae has convinced me that these two species are distinct. They are, however, sometimes difficult to distinguish in pinned material, and further study may necessitate changes in the records of distribution.

- Shining yellow; tips of second, third, and fourth veins clouded. N. H., Vt., Mass., R. I., Conn., N. Y., N. J., Pa., O., Md., Va. *quinaria* Loew.
20. Carina minute; small prescutellars present; wings much clouded. N. H., Vt., Mass., N. Y., N. J., Ill., Minn., Wash. *inversa* Walker.
- Carina usual size; prescutellars not differentiated; wings clear or with small clouds along veins. 21.
21. Mesonotum yellow, with distinct reddish longitudinal stripes; second orbital nearly as long as third. N. H., Mass., Conn., N. Y., N. J., Pa., Md., D. C., Va., W. Va., Fla., Ala., La., Ind., Ill., Ore., Calif., Cuba, Australia, (Kans.—Kahl; Minn.—Coquillett; Canaries, Europe, S. Africa — Becker, Ville-neuve, as *D. rubrostriata* Becker¹) *busckii* Coquillett.
- Mesonotum light gray, with numerous dark brown spots; carina sulcate. Mass., R. I., N. Y., N. J., Pa., Md., D. C., Va., Tenn., Fla., Ala., La., Tex., Ind., Mo., Ark., Calif.; Bermuda, Bahamas, Cuba, Jamaica, Hayti, Porto Rico, Dominica, Barbados, Mexico, Brit. Honduras, Costa Rica, Panama, Brazil; Hawaii, E. Africa, (Canaries — Becker; Austria, W. Africa — Mik; Java — Van der Wulp, as *D. nigropunctata* Van der Wulp) . . *repleta* Wollaston.
- Mesonotum not distinctly marked. 22.
22. Costal index about 1.0; fourth vein index about 5.5; pleuræ with a dark stripe above. Ala., Ga. *quadrata* Sturtevant.
- Costal index 2.0 or over; fourth vein index less than 3.0; no pleural stripe. . 23.
23. Blackish species, not at all yellowish or reddish. 24.
- Yellow or reddish brown. 25.
24. Costal index about 4.0; $2\frac{1}{2}$ mm. long; no combs on tarsi. Mass., N. Y., Md., Va., Ark., Ala. *robusta* Sturtevant.
- Costal index about 2.7; 2 mm. long; a comb of short stout black bristles on each of the two basal joints of the first tarsi of the male. Europe, Ore., Calif. *obscura* Fall.
25. Costal index less than 3.0; fourth vein index about 2.3; the male has a comb of short stout black bristles on the basal tarsal joint of the first leg. Nova Scotia to Wash., south to Chile; Europe, Africa, Australia, Hawaii. The species is apparently to be found everywhere except in very cold regions. *melanogaster* Meigen.
- Costal index over 3.5; fourth vein index less than 1.5; no tarsal combs. . . 26.
26. Dull yellow, not at all reddish; a row of very short, stout bristles on lower apical part of front femur; wings slightly clouded on posterior crossvein and tips of first and second veins. Mass., N. Y., N. J., O., Fla., Ala., La., Calif., Costa Rica, (Canaries — Becker) *tripunctata* Loew.
- Reddish brown; no combs on femora; wings clear, or occasionally slightly clouded on posterior crossvein. Quebec, N. H., Vt., Mass., R. I., Conn., N. Y., N. J., Pa., O., Ind., Ill., Md., D. C., Va., Ga., Ala., Wis., S. Dak., Alberta, Brit. Columbia, Kans., N. Mex., Calif.; Mexico, Trinidad (W. I.), Europe, Australia. *funebri* Fabricius.

¹ Mr. F. Knab pointed out this synonymy to me in the first instance. The species is surely cosmopolitan.

Drosophila duncani, new species

Arista with six branches above and two below. Antennæ yellow, third joint darker, long, and clothed with long yellow hairs. Front over one-third the width of the head, wider above; reddish yellow, orbits and triangle grayish. Second orbital about half the third, which is scarcely over half the first. Carina quite narrow, confined to the upper part of the face. Face and cheeks yellow. Second oral bristle scarcely half the vibrissa. Greatest width of cheeks about one-sixth greatest diameter of eyes. Eyes with short fine pile.

Acrostichal hairs in six rows; no prescutellars. Mesonotum and scutellum dull yellowish brown. Pleuræ yellow, brownish above. Legs pale yellow. Apical and preapical bristles on first and second tibiæ, preapicals on third.

Abdomen yellow, each segment with a dark brown posterior band, thickened in the middle.

Wings clear. Costal index about 3.8; fourth vein index about 1.4; 5x index about 1.2; 4c index about 0.9.

Length body $2\frac{1}{4}$ mm.; wings $2\frac{1}{2}$ mm.

Type and three paratypes, Flat Rock, Ill., 1915, "Fungus" (Dr. F. N. Duncan). The type is deposited in The American Museum of Natural History.

The following Nearctic species are listed in Aldrich's Catalogue but are not included in the tables above. The synonymy is not new.

Drosophila albipes Walker. Not recognizable from the description.

D. ampelophila Loew = *melanogaster* Meigen.

D. apicata Thomson = *Scaptomyza terminalis* Loew.

D. brevis Walker. Not recognizable from the description.

D. colorata Walker. May be same as *sulcata* Sturtevant. Uncertain.

D. confusa Stæger. Does not occur in Nearctic region. Records are based on *D. affinis* Sturtevant.

D. decemguttata Walker. Probably not *Drosophila*. (*Diastata*?)

D. flaveola Meigen. Does not occur in Nearctic. Is a *Scaptomyza*.

D. fronto Walker. Not recognizable from the description.

D. linearis Walker. Probably not *Drosophila*. (*Scaptomyza*? Geomyzid?)

D. minuta Walker. Not recognizable from the description.

D. multipuncta Loew = *guttifera* Walker.

D. punctulata Loew = *repleta* Wollaston.

D. quadrimaculata Walker = *Leucophenga varia* Walker.

D. valida Walker = *Minettia macula* Loew.

Article XV.—STUDIES IN COMPARATIVE MYOLOGY AND OSTEOLOGY.¹ NO. III

BY W. K. GREGORY AND C. L. CAMP

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INTRODUCTION

BY W. K. GREGORY

The palæontological collections of the world contain great numbers of fossil skeletons which have been described minutely and accurately, but seldom with any detailed reference to the muscles that once moved them. In general, comparative osteology and palæontology are treated in one set of works and comparative myology in another; with few exceptions these

¹ Conducted under the direction of William K. Gregory, Ph.D., Assistant Professor of Vertebrate Palæontology, Columbia University, and Associate in Palæontology, The American Museum of Natural History.

lines of study have been pursued by different workers having little knowledge of each other's results. Only in a very few instances have attempts been made to reconstruct the probable arrangement of the limb muscles in certain extinct animals, as in von Huene's reconstruction of *Plateosaurus* and Lull's reconstruction of *Stegosaurus*, but no wide application of comparative myological results to palæontological material has as yet come to our notice.¹

The objects of the present paper are, first, to make more available to palæontologists the treasures of comparative myology by presenting a convenient introduction to the subject, and, second, to suggest that, when the muscles are taken into consideration, the skeletal elements of both recent and extinct vertebrates acquire a new and manifold interest.

More in detail, the objects of these studies are to review the homologies of similar muscles in the different vertebrate classes; to make restorations of the musculature of the jaws, limbs, and axial skeleton of certain extinct amphibians, reptiles, and mammals; and to discover one by one some of the stages by which the more specialized mechanisms of the higher vertebrates were evolved.

Much has been done by students of comparative myology to make our task practicable. Fürbringer and Gadow especially, in their splendid studies, have collated the literature of the limb muscles of amphibians, reptiles, and birds and clarified the subject greatly by their excellent dissections, critical discussions, and summaries. On the mammalian side, we have used especially the studies of Wilson, McKay, Westling, and Coues on the myology of the monotremes, the "Planches de Myologie" of Cuvier and Laurillard, the accurate text-book of Reighard and Jennings on the cat, Cunningham's "Text-Book of Anatomy," Weisse's "Practical Human Anatomy," and the comparative studies of Windle and Parsons on the myology of the Carnivora and of the Ungulata.² With such data before us, we have attempted a general review and summary of the probable homologies of the pectoral and pelvic muscles in reptiles and mammals, which is a necessary preliminary for our restoration of these parts in *Cynognathus*, as well as for further considerations concerning the evolution of the locomotor organs of vertebrates.

The illustrations for the present paper have been prepared by Mrs. E. M.

¹ Watson's paper (Oct. 1917) on the evolution of the tetrapod shoulder-girdle and fore-limb, which was received too late for extended discussion in this paper, forms an important exception to this statement.

² It is scarcely necessary to add that we have also endeavored, so far as possible, to gain practical knowledge of the subject by dissecting reptiles and mammals for ourselves.

Fulda under the direction of the authors. For the convenience of readers, we have included in our illustrations a selected series of drawings of the musculature of recent reptiles, copied from the works of Fürbringer and Gadow.

Although our observations and conclusions have been frequently revised and reconsidered by us during the last two years, we have no doubt failed to detect all of our own errors in so complex and difficult a subject. Nevertheless, further delay seems inadvisable and we therefore venture to submit our still imperfect results to the critical consideration of anatomists and palæontologists.

The first contribution to these "Studies" was a series of reconstructions of the musculature of the head, vertebral column, and limbs of Eocene and Oligocene titanotheres by W. K. Gregory, assisted by Erwin S. Christman. This will be published in Professor Osborn's monograph on the titanotheres. The second was a memoir on the homologies and functions of the jaw muscles of vertebrates by L. A. Adams, which is now in press (*Ann. N. Y. Acad. Sci.*, 1918). The third is the present paper. The fourth (in progress) is a review of the adaptive radiation of the locomotor apparatus in recent and extinct reptiles, by W. K. Gregory. The fifth (in progress) is a review of the limb muscles of recent amphibians, with an attempted reconstruction of the limbs of *Eryops*, a Permian stegocephalian, by R. W. Miner. The work has been done by, or under the direction of, the senior author of the present paper in the Department of Vertebrate Palæontology of this Museum; it has resulted from the cooperation of the Museum, including members of the staff, with graduate instruction and research in the Department of Zoology, Columbia University. This cooperation was originated by Professor Osborn and President Seth Low in 1891.

To Professors Osborn, Huntington, and Schulte, and to Dr. W. D. Matthew, the authors are indebted both for material and for counsel.

PART I.—A COMPARATIVE REVIEW OF THE MUSCLES OF THE
SHOULDER-GIRDLE AND PELVIS OF REPTILES AND MAMMALS,
WITH AN ATTEMPTED RECONSTRUCTION OF THESE PARTS
IN *CYNOGNATHUS*, AN EXTINCT THERAPSID REPTILE

By W. K. GREGORY AND C. L. CAMP

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REVIEW AND IDENTIFICATION OF THE MUSCLES OF THE SHOULDER-GIRDLE

By C. L. Camp

Origins, Insertions, and Innervations of Muscles Inserted upon the Scapula and Coracoid in Recent Placentals, Monotremes, and Reptiles,
with Inferred Conditions in *Cynognathus*

The muscles running from the neck and flanks to the shoulder-girdle fall into two groups, each group comprising three successive layers, as follows:

I.—Cervical Region

Outermost layer	$\left\{ \begin{array}{l} \text{trapezius} \left\{ \begin{array}{l} \text{clavo-} \\ \text{acromio-} \\ \text{spino-} \end{array} \right. \\ \\ = \text{cucullaris of } Sphenodon \end{array} \right.$
Second layer $\left\{ \begin{array}{l} \text{lateral} \\ \text{dorsal} \end{array} \right.$	$\left\{ \begin{array}{l} \text{omotrachelian} \\ = \text{lev. scap. superf. sup. + inf.} \\ \text{rhomboideus} \end{array} \right.$
Third layer $\left\{ \begin{array}{l} \text{dorsal} \\ \text{and} \\ \text{ventral} \end{array} \right.$	$\left\{ \begin{array}{l} \text{levator scapulæ} \\ (= \text{levator scap. prof.}) \end{array} \right.$

II.—Dorsal Region

Outermost layer	latissimus dorsi
Second layer, lateral	serratus anterior superficialis (serial homologue of omotrachelian)
Third layer, lateral	serratus anterior profundus

In the following pages the names applied to the muscles of placental mammals are set in heavy faced type at the head of each section, followed by the names of muscles in the lower animals which are more or less homologous with them.

Trapezius

CARNIVORA (Windle and Parsons, 1897, p. 385)

Clavo-trapezius

Origin.—Curved line of occiput and ligamentum nuchæ.

Insertion.—Clavicle, on tendinous intersection between this muscle and the deltoid.

Acromio-trapezius

Origin.—Ligamentum nuchæ and spines of anterior thoracic vertebræ.

Insertion.—Anterior border of spine and acromion.

Spino-trapezius

Origin.—Spines of posterior thoracic vertebræ.

Insertion.—Dorsal end of scapular spine.

Innervation.—(Cat) N. accessorius.

MONOTREMES (McKay, 1894, pp. 323–326)

Trapezius anterior (Pls. XLI, *trap.*; XLII)

Origin.—Parietal bone and ligamentum nuchæ.

Insertion (*Ornithorhynchus*).—Anterior extremity of vertebral border of scapula, medial border of spine and acromion, and outer fourth of anterior surface of clavicle.

Trapezius posterior (Pl. XLI, *trap.*)

Origin.—Spines of dorsal vertebræ and dorsal surface of posterior ribs.

Insertion (*Ornithorhynchus*).—Anterior extremity of vertebral border.

Innervation.—N. accessorius.

CYNOGNATHUS (inferred conditions)

Trapezius anterior (Pls. XXXIX, *trap.*; XL, XLI, XLII)

Origin.—As in monotremes.

Insertion.—Spine, acromion and clavicle.¹

¹ Text continued on page 464.

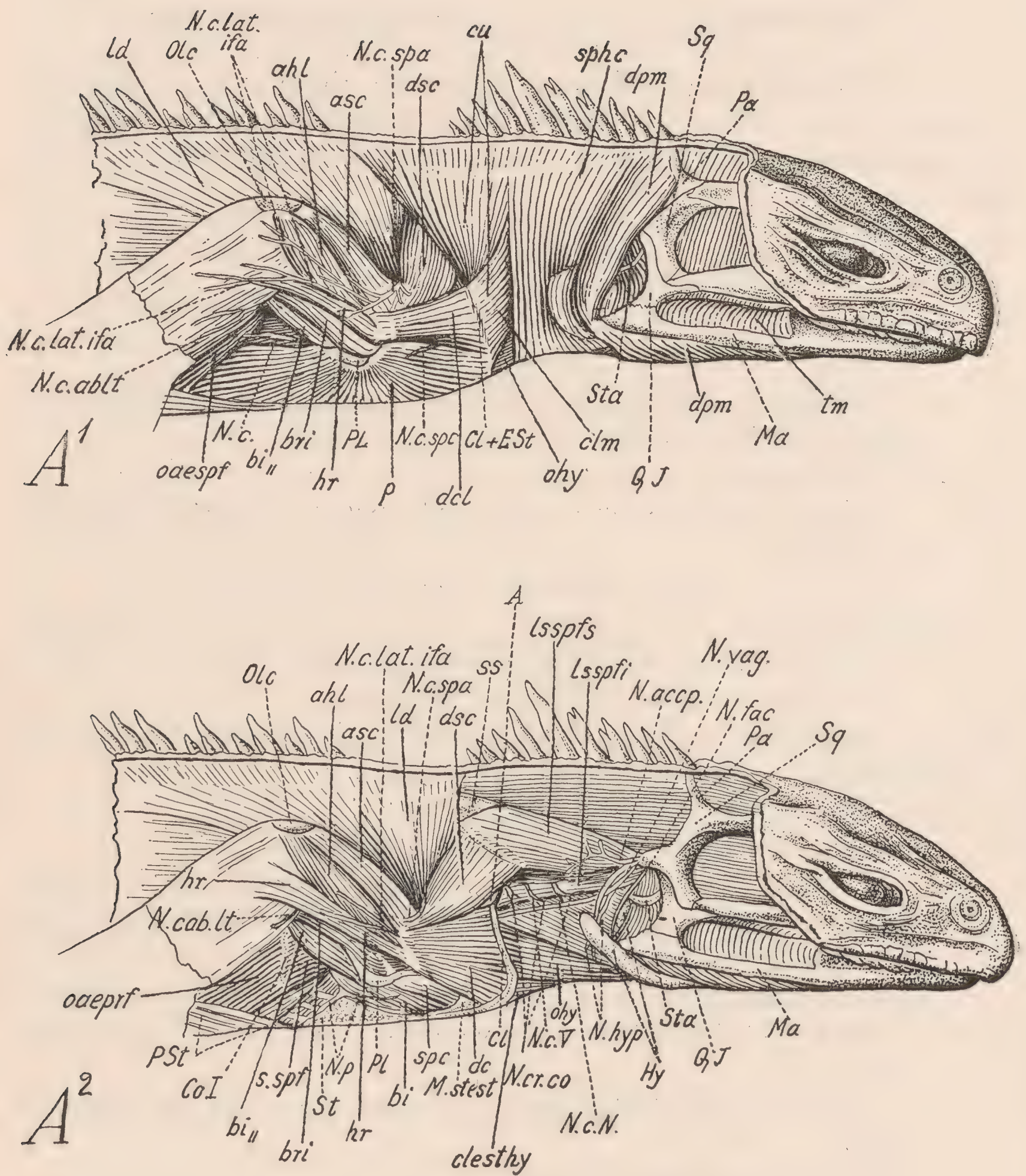


Fig. 1.

Fig. 1. *Sphenodon punctatus*. Pectoral musculature. After Fürbringer 1900.A¹. After removal of the skin.

Abbreviations (Fürbringer)

<i>tm.</i>	temporo-masseter	<i>N. c.</i>	nervous cutaneus
<i>dpm.</i>	depressor mandibulæ	<i>N. c. spa.</i>	nervus cutaneus axillaris supra anconeus
<i>spnc.</i>	sphincter colli	<i>N. c. lat. ifa.</i>	nervus cutaneus brachii et ante- brachii superior lateralis infra anconeus
<i>cu.</i>	cucullaris	<i>N. c. ablt.</i>	nervus cutaneus antebrachii later- alis
<i>dsc.</i>	dorsalis scapulæ	<i>N. c. spc.</i>	nervus cutaneus supracoracoideus
<i>ld.</i>	latissimus dorsi	<i>Ma.</i>	malar
<i>asc.</i>	anconeus scapularis	<i>Sta.</i>	stapes
<i>ahl.</i>	anconeus humeralis lateralis	<i>Sq.</i>	squamosal
<i>hr.</i>	humero-radialis	<i>Q. J.</i>	quadrato-jugal
<i>ohy.</i>	omohyoideus	<i>Pa.</i>	parietal
<i>clm.</i>	cleidomastoideus	<i>Cl. + Est.</i>	clavicle + episternum (interclavicle)
<i>dcl.</i>	deltoides clavicularis	<i>PL.</i>	processus lateralis humeri
<i>p.</i>	pectoralis	<i>Olc.</i>	olecranon (patella ulnaris)
<i>oaespf.</i>	obliquus abdominis externus super- ficialis		
<i>bri.</i>	brachialis internus		
<i>bi.</i>	biceps, distal belly		

A². After removal of the sphincter colli, cucullaris, cleidomastoideus and pectoralis.Abbreviations as in A¹, also:

<i>lsspfs.</i>	levator scapulæ superficialis superior	<i>St.</i>	sternum
<i>SS.</i>	suprascapular	<i>PSt.</i>	parasternum (gastralia)
<i>lsspfi.</i>	levator scapulæ superficialis inferior	<i>N. fac.</i>	nervus facialis
<i>dc.</i>	deltoides clavicularis	<i>N. vag.</i>	nervus vagus
<i>clesthy.</i>	cleido episternalis hyoideus	<i>N. accp.</i>	nervus accessorius posterior
<i>spc.</i>	supracoracoideus	<i>N. hyp.</i>	nervus hypoglossus
<i>bi.</i>	biceps, proximal belly	<i>Nc. N.</i>	an error; should be <i>N. c. IV.</i>
<i>sspf.</i>	serratus superficialis	<i>N. c. IV. }</i>	nervi cutanei of the thorax
<i>oaepf.</i>	obliquus abdominis externus pro- fundus	<i>N. c. V. }</i>	
<i>Hy.</i>	os hyoideum	<i>N. cr. co.</i>	rami musculi cucullaris (from the cervical nerves)
<i>A.</i>	acromion (processus clavicularis)	<i>N. c. spa.</i>	ramus cutaneus nervi supracora- coidei
<i>M. stest.</i>	membrana sterno-episternalis	<i>N. p.</i>	nervus pectoralis
<i>CL.</i>	clavicle		
<i>Co. I.</i>	1st rib (Costa I)		

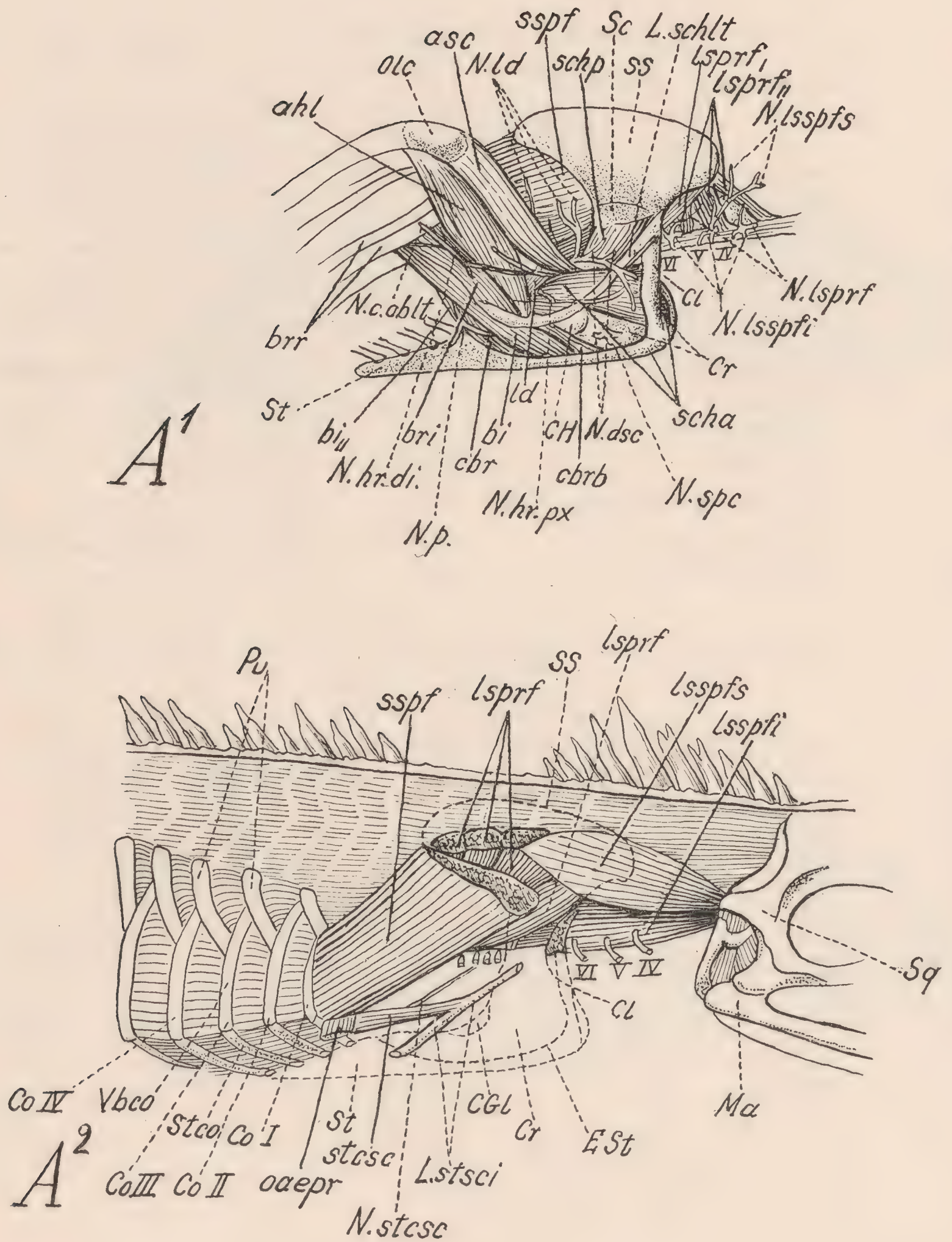


Fig. 2.

Fig. 2. A¹. *Sphenodon punctatus*. Deep muscles of the shoulder-girdle. After Fürbringer 1900.

Abbreviations as in previous figures; also:

<i>lsprf.</i>	levator scapulæ et serratus profundus, superficial layer	<i>IV, V, VI.</i>	spinal nerves
<i>lsprf.</i>	levator scapulæ et serratus profundus, deep layer	<i>N. lssps.</i>	nerve for the levator scapulæ superficialis superior
<i>scha.</i>	scapulohumeralis anterior	<i>N. lsspfi.</i>	nerve for the levator scapulæ superficialis inferior
<i>schp.</i>	" posterior	<i>N. lsprf.</i>	nerve for the levator scapulæ et serratus profundus
<i>sspf.</i>	serratus superficialis	<i>N. spc.</i>	nerve for the supracoracoideus
<i>ld.</i>	tendon of latissimus dorsi	<i>N. dsc.</i>	nervus musc. dorsalis scapulæ (N. axillaris posterior)
<i>bi.</i>	biceps (proximal belly)	<i>N. hr. px.</i>	proximal nerve for the musc. humero-radialis
<i>cbr.</i>	coracobrachialis	<i>N. ld.</i>	nervus musc. latissimi dorsi
<i>cbrb.</i>	coracobrachialis brevis	<i>N. hr. di.</i>	distal nerve for the musc. humero-radialis
<i>brr.</i>	brachio-radialis (M.supinator longus)	<i>N. p.</i>	nervus pectoralis
<i>CH.</i>	caput humeri		
<i>L. schlt.</i>	ligamentum scapulohumeralis lateralis		
<i>Cr.</i>	coracoid, with supracoracoid nerve		

A². Deepest muscles of the shoulder. After the removal of the pectoral girdle.

Abbreviations as in preceding figures; also:

<i>stcsc.</i>	m. sternocosto-scapularis	<i>Vbco.</i>	vertebro-costale (vertebral part of rib)
<i>oaepr.</i>	obliquus abdominis externus profundus	<i>Stco.</i>	sternocostale (sternal part of rib)
<i>ESt.</i>	episternum [interclavicle]	<i>Pu.</i>	processus uncinatus
<i>CGL.</i>	glenoid facet of coracoid	<i>IV, V, VI.</i>	spinal nerves
<i>L. stsci.</i>	ligamentum sternoscapularis	<i>N. stcsc.</i>	nervus musc. sternocosto-scapularis
<i>Co. I, II, III, IV.</i>	costa I, II, III, IV		

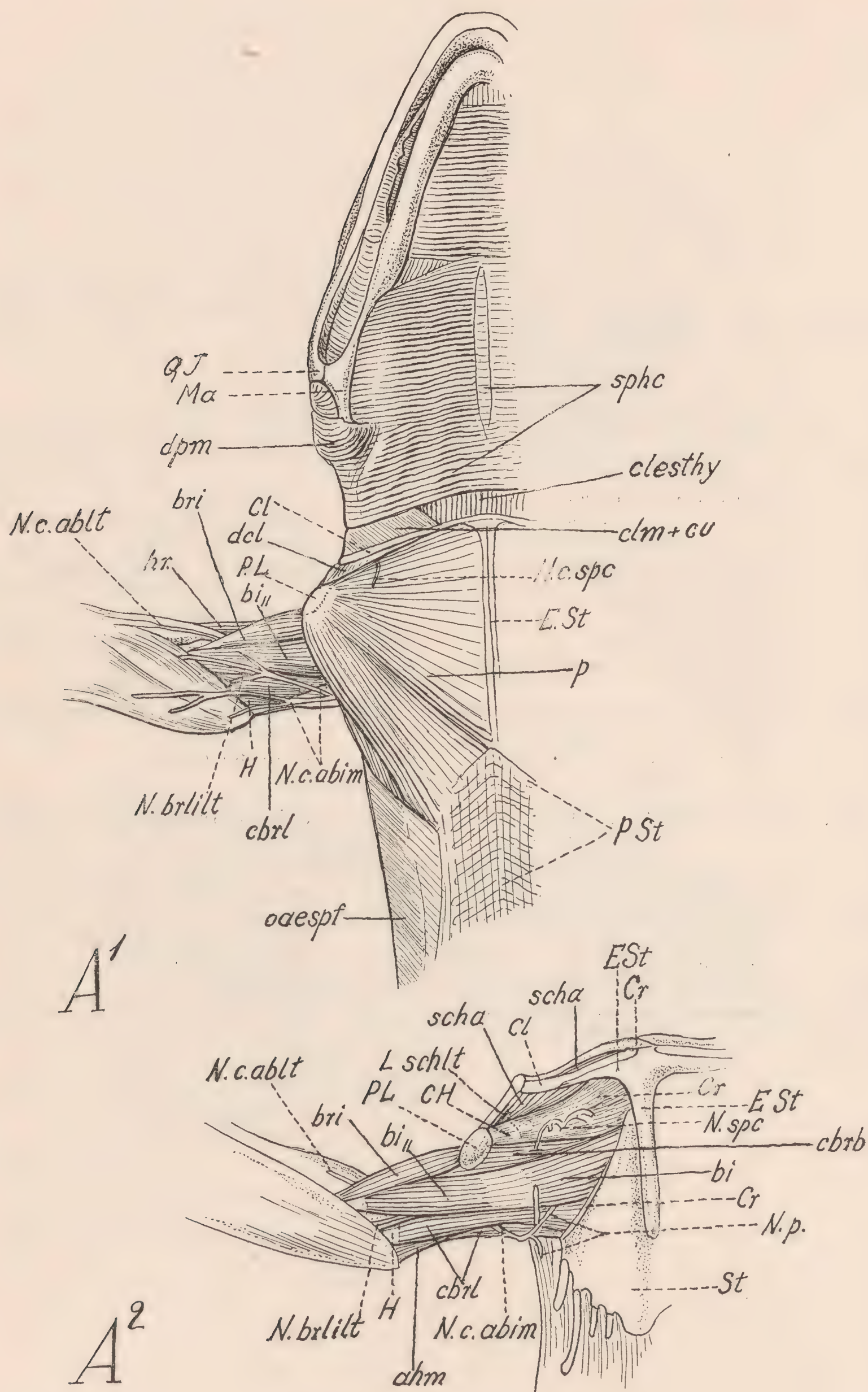


Fig. 3.

Fig. 3. *Sphenodon punctatus*. Pectoral musculature, ventral views. After Fürbringer 1900.

A¹. Superficial muscles.

<i>sphc.</i>	sphincter colli	<i>hr.</i>	humero-radialis
<i>dpm.</i>	depressor mandibulæ	<i>cbrl.</i>	coracobrachialis longus
<i>clesthy.</i>	cleido episternalis hyoideus	<i>H.</i>	humerus
<i>clm.+cu.</i>	cleidomastoideus+cucullaris	<i>N. c. abim.</i>	nervus cutaneus brachii et ante- brachii inferior medialis
<i>dcl.</i>	deltoides clavicularis	<i>N. brlitt.</i>	nervus brachialis longus inferior lateralis (N. musculo-cutaneus et medianus et profundus)
<i>p.</i>	pectoralis	<i>N. c. ablt.</i>	nervus cutaneus antebrachii lateralis
<i>oaespf.</i>	obliquus abdominis externus super- ficialis		
<i>bi.</i>	biceps, distal belly		
<i>bri.</i>	brachialis internus		

A². Deep muscles of the axillary region.

Abbreviations as in preceding figures; also:

<i>N. p.</i>	nervus pectoralis	<i>L. schlt.</i>	ligamentum scapulohumeralis lateralis
<i>CH.</i>	caput humeri	<i>ahm.</i>	anconeus humeralis medialis
<i>PL.</i>	processus lateralis humeri		

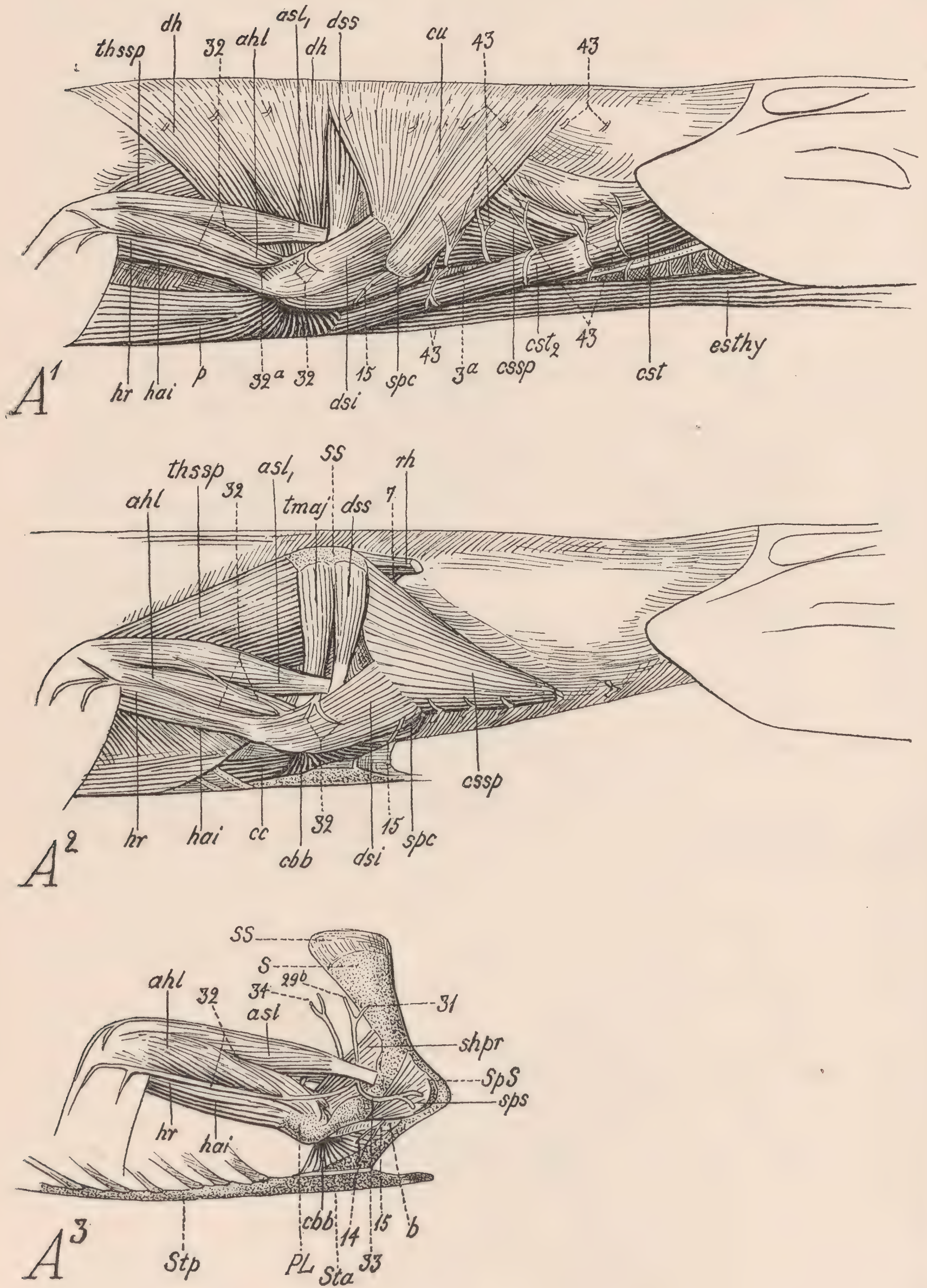


Fig. 4.

Fig. 4. *Crocodylus acutus*. Pectoral musculature. After Fürbringer 1876.

A¹. After the removal of the sphincter colli.

<i>cu.</i>	cucullaris (trapezius)	<i>ahl.</i>	anconeus humeralis lateralis
<i>dss.</i>	dorsalis scapulæ (deltoides scapularis superior)	<i>hai.</i>	humero-antebrachialis inferior (brachialis inferior)
<i>dh.</i>	dorso-humeralis (latissimus dorsi)	<i>hr.</i>	humero-radialis
<i>thssp.</i>	thoraci-scapularis superficialis (serratus superficialis)	<i>p.</i>	pectoralis
<i>esthy.</i>	episterno-hyoideus	<i>43.</i>	cutaneous and muscular branches, arising neither from spinal nerves nor from the plexus brachialis
<i>cst</i> }	capiti-sternalis (sterno-mastoideus)	<i>3a</i>	N. thoracicus anterior (V in <i>Crocodylus</i>)
<i>cst</i> ₂ }		<i>15</i>	cutaneous branch of N. supracoracoideus
<i>cssp.</i>	collo-scapularis superficialis (levator scapulæ superficialis)	<i>32</i>	parts of N. axillaris (Nn. cutaneus brachii superior lateralis)
<i>spc.</i>	supracoracoideus	<i>32a</i>	N. humero radialis
<i>dsi.</i>	deltoides scapularis inferior		
<i>asl</i> ₁	anconeus scapularis lateralis externus		

A². After the removal of the cucullaris, latissimus dorsi, pectoralis, capiti-sternalis and episterno-hyoideus.

Abbreviations as in A¹; also:

<i>t. maj.</i>	"M. teres major" [of doubtful homology]	<i>ss.</i>	suprascapula
<i>rh.</i>	rhomboideus	<i>7</i>	hinder branch of N. thoracicus superior (VII)
<i>cbb.</i>	coracobrachialis brevis		
<i>cc.</i>	costo coracoideus		

A³. After the removal of the "teres major" (*t. maj.*), deltoides scapularis inferior (*dsi.*), deltoides scapularis superior (*dss.*) and pars coracoidea of the M. supracoracoscapularis (*spc.*).

Abbreviations as in A¹ and A² also:

<i>sps.</i>	pars scapularis of M. supracoracoscapularis	<i>Stp.</i>	posterior part of sternum
<i>b.</i>	biceps, proximal belly	<i>31</i>	N. dorsalis scapulæ (posterior)
<i>shpr.</i>	scapulohumeralis posterior	<i>29b</i>	N. teres major
<i>S.</i>	scapula	<i>34</i>	Nn. latissimi dorsi
<i>SpS.</i>	spina scapulæ	<i>33</i>	branch of N. axillaris for M. deltoides inferior
<i>PL.</i>	processus lateralis humeri	<i>15</i>	cutaneous branch of N. supracoracoideus
<i>Sta.</i>	anterior part of sternum	<i>14</i>	muscular " " " "

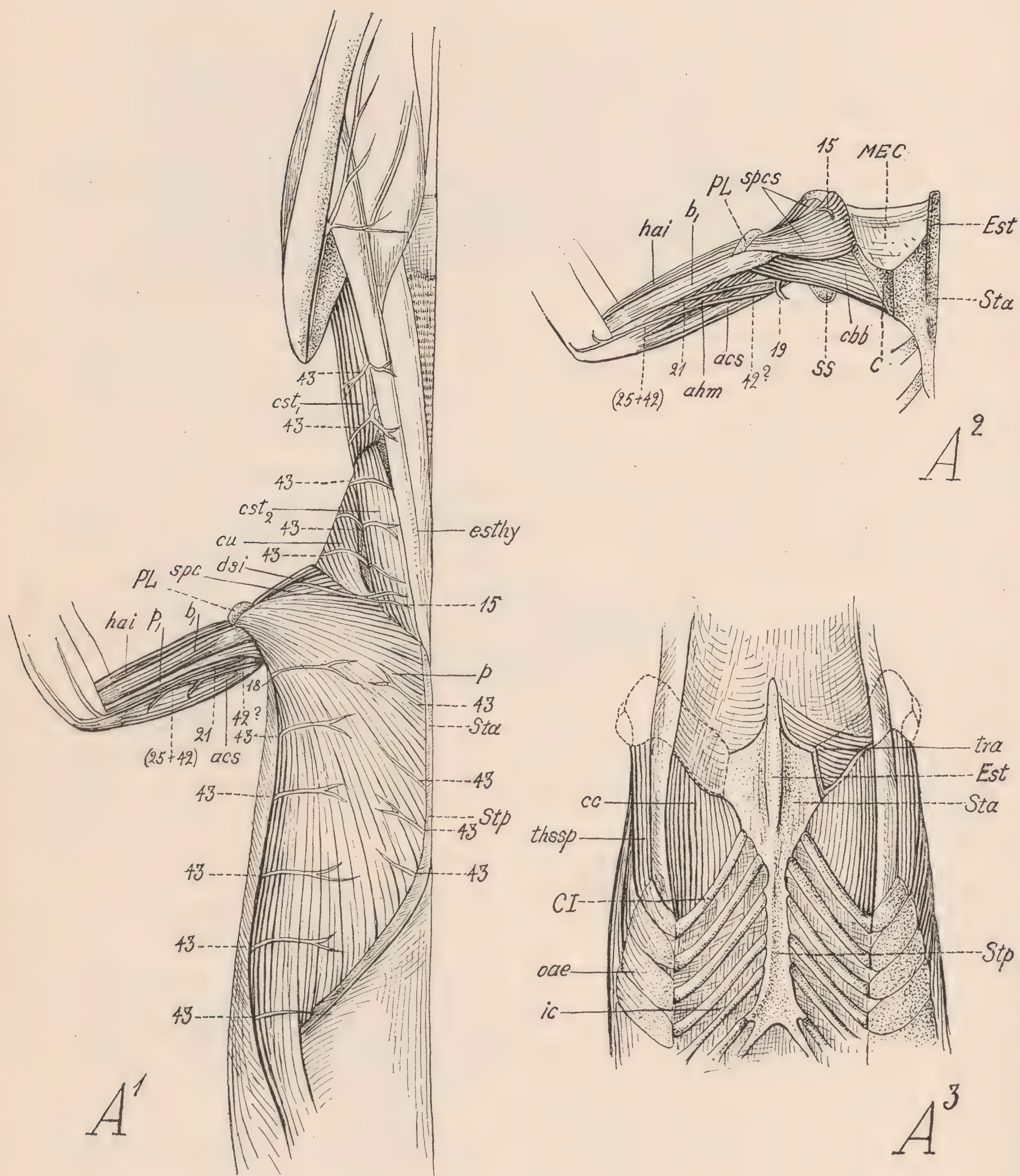


Fig. 5.

Fig. 5. Pectoral musculature of *Crocodilus acutus*. After Fürbringer 1876.

A¹. Ventral view after removal of the skin and of the sphincter colli.

<i>cst₁ cst₂</i>	capiti-sternalis	<i>Sta, Stp.</i>	sternum, anterior and posterior por-
<i>cu.</i>	cucullaris		tions
<i>p.</i>	pectoralis, <i>p₁</i> separate slip of same	<i>PL.</i>	processus lateralis humeri
<i>dsi.</i>	deltoides scapularis inferior		Nerves as in Fig. 4; also:
<i>spc.</i>	supracoracoideus	18	N. cutaneus pectoralis
<i>b₁</i>	biceps (distal belly)	21	N. brachialis longus inferior
<i>hai.</i>	humero-antebrachialis inferior (brachialis inferior)	(25 + 42)	N. cutaneus brachii et antebrachii medialis
<i>acs.</i>	anconeus coracoscapularis	43	(See p. 459)

A². Ventral view of the deep muscles of the right shoulder after the removal of the pectoralis, cucullaris, deltoides scapularis inferior.

Abbreviations as in A¹; also:

<i>spcs.</i>	M. supracoracoscapularis	<i>SS.</i>	suprascapula
<i>cbb.</i>	coracobrachialis brevis	19	N. pectoralis
<i>MEC.</i>	membrana episterno-coracoideus	15	cutaneous branch of <i>N. supracoracoideus</i>
<i>C.</i>	coracoid		

A³. Deepest muscles of the pectoral region, ventral view.

<i>tra.</i>	transversus abdominis	<i>ic.</i>	intercostales
<i>cc.</i>	costo coracoideus	<i>Est.</i>	episternum [interclavicle]
<i>thssp.</i>	thoracoscapularis superficialis (serratus anterior superficialis)	<i>Sta., Stp.</i>	sternum, anterior and posterior por-
<i>oae.</i>	obliquus abdominis externus		tions
		<i>CI.</i>	costa inferior [gastralium]

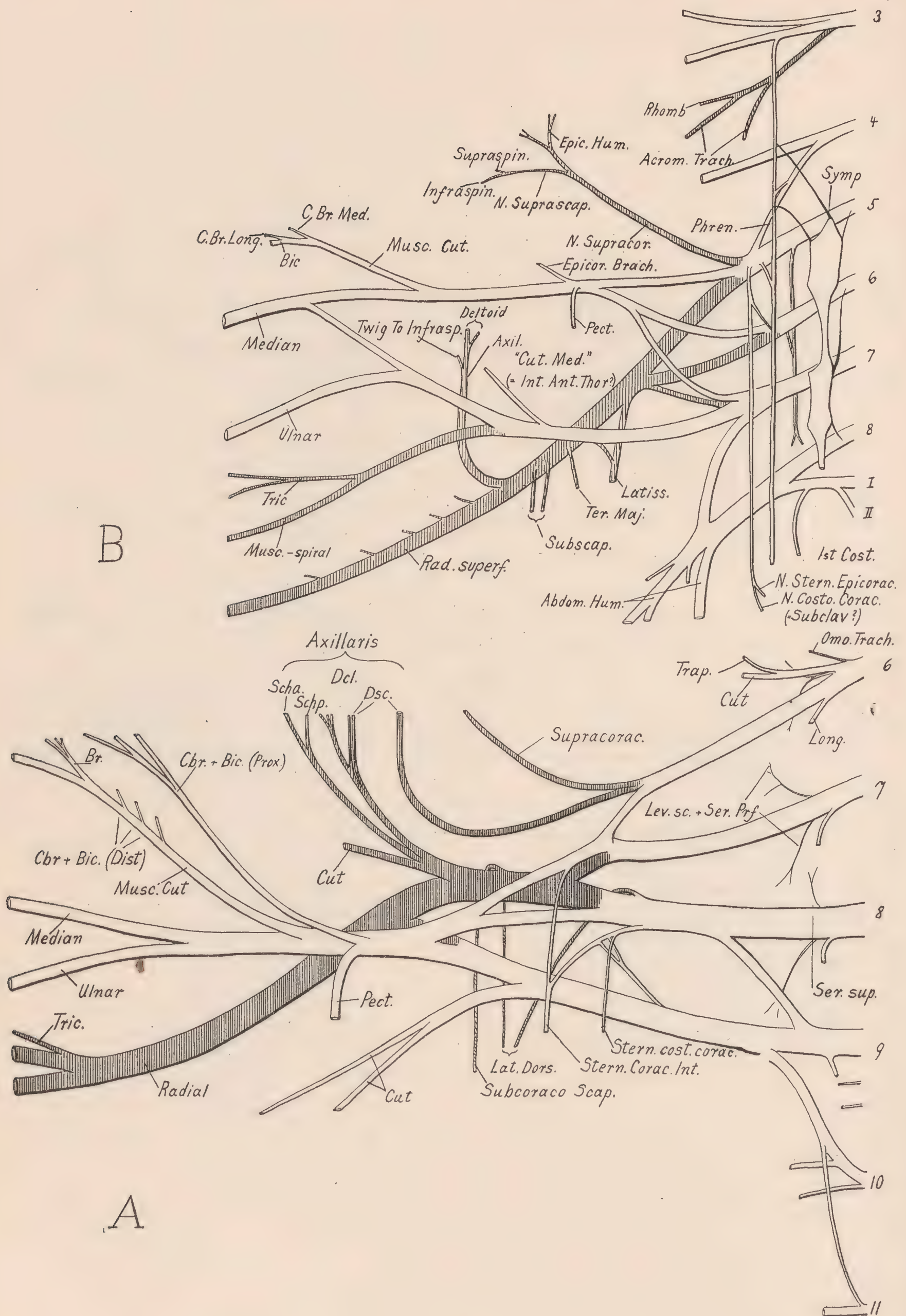


Fig. 6.

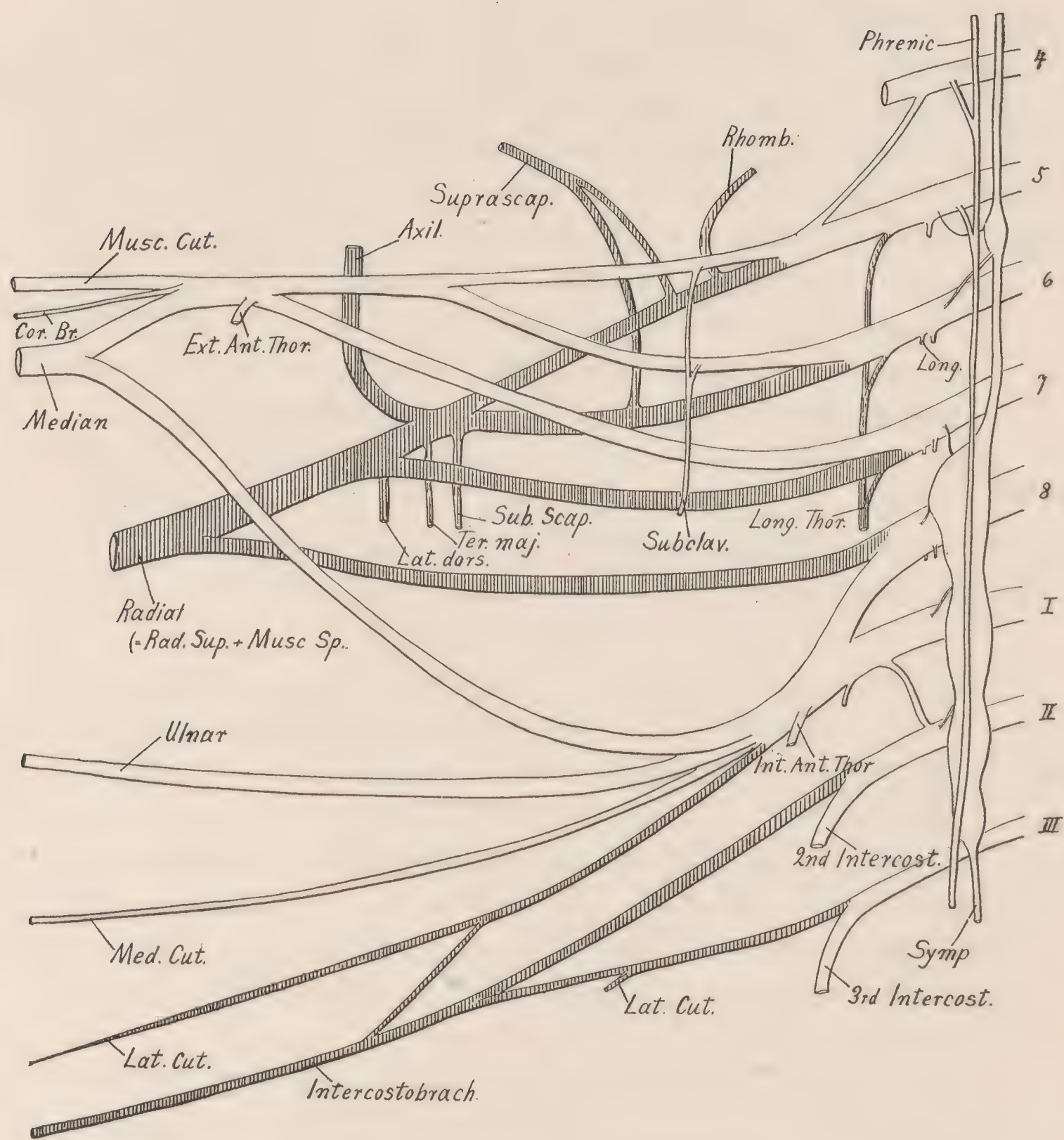


Fig. 7. Brachial plexus of Man. Generalized from Cunningham, 1903, and from Hardesty in Morris and McMurrich. [C. L. C.] Cf. Fig. 6.

Fig. 6. Brachial plexus of (A) *Sphenodon*, generalized from Fürbringer, 1900, and (B) *Ornithorhynchus*, generalized from McKay, 1894. [C. L. C.]

Superior brachial nerves cross hatched; inferior brachial and inferior thoracic nerves white.

Trapezius posterior (Pls. XXXIX, *trap.*; XL, XLI, XLII)

Origin.—As in monotremes.

Insertion.—Spine of scapula.

Remarks.—It seems probable that in *Cynognathus* the eversion of the border of the scapula interrupted the continuous “cucullaris” of *Sphenodon* and caused the primary differentiation of that muscle into acromial and spinous divisions.

SPHENODON (Fürbringer, 1900, pp. 462–464)

Trapezius (capiti-dorso-clavicularis, cucullaris) (Fig. 1, *cu.*)

Origin.—Parietal and squamosal bones.

Insertion.—Lateral two-thirds of clavicle and the “acromion.”

Innervation.—N. accessorius, ramus externus.

Rhomboideus

CARNIVORA (Windle and Parsons, 1897, pp. 386–388)

Rhomboideus anterior

Origin.—Occiput and ligamentum nuchæ.

Rhomboideus posterior

Origin.—Spines of anterior thoracic vertebræ.

Insertion.—Vertebral border of scapula.

Innervation.—(Cat) sixth cervical nerve.

(Man) fourth or fifth cervical nerve.

ORNITHORHYNCHUS (McKay, 1894, p. 336)

Rhomboideus anterior (Pl. XLI, *rhomb.*)

Origin.—Parietal bone and ligamentum nuchæ.

Rhomboideus posterior

Origin.—Ligamentum nuchæ in region of spine of fifth cervical vertebra.

Insertion.—Posterior half of vertebral border.

Innervation.—Third cervical nerve.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLI, XLII)

Origin.—Ligament or fascia above spines of cervical vertebræ.

Insertion.—Anterior vertebral angle of scapula and suprascapula.

CROCODILE (Fürbringer, 1876, pp. 779–780, and 1900, p. 501) (Fig. 4, *rh.*)

Origin.—Fascia above eighth and ninth vertebræ.

Insertion.—Anterior two-thirds of dorsal inner surface of supra-scapula.

Innervation.—N. thoracalis superioris VII.

Remarks.—According to Fürbringer this muscle (Fig. 4, *rh.*), which

occurs only in the Crocodilia among recent Reptilia, is probably differentiated from the omotrachelian and levator scapulæ complex. Its presence in *Cynognathus* is suggested by the large size of the head and by the presence of an impression, on the anterior corner of the vertebral border of the scapula, which bears marks of a muscle insertion probably distinct from that of the serratus.

SPHENODON

Not present as such.

Omotrachelian

PLACENTALS

(= *Levator scapulæ ventralis*)

Origin.—Transverse process of atlas.

Insertion.—Acromion, near tubercle.

Innervation.—(Cat) third cervical nerve.

(Carnivora, "several cervical nerves" Windle and Parsons).

ORNITHORHYNCHUS (McKay, 1894, pp. 343–344)

Dorsal portion (Pl. XLII, *omotr. dors.*)

Origin.—Distal extremity of external border of hypapophysis of atlas.

Insertion.—Upper part of spine and anterior half of vertebral border of scapula.

Ventral portion (Pl. XLII, *omotr. vent.*)

Origin.—Distal extremity of ventral surface of hypapophysis of atlas.

Insertion.—Ventral two-thirds of spine and adjacent inner surface of scapula, inner border and surface of acromion, and distal part of dorsal face of clavicle.

Innervation.—Third cervical nerve.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, *omotr.*; XLI, XLII)

Origin.—Transverse process of atlas.

Insertion.—Lateral half of anterior surface of spine ("supraspinous fossa"), antero-dorsal surface of acromion, and outer side of anterior one-third of suprascapula.

SPHENODON (Fürbringer, 1900, pp. 464–466)

Levator scapulæ superficialis superior (Fig. 1, *A*², *lsspfs.*)

Origin.—Transverse processes of first (chiefly) and second cervical vertebrae.

Insertion.— Anterior two-thirds of outer side of suprascapula.
Levator scapulæ superficialis inferior (Fig. 1, *A*², *lssphi.*)

Origin.— With above.

Insertion.— Anterior border of scapula near “acromion” and dorsal end of clavicle.

Innervation.— Nn. spinales IV, V, and VI.

Remarks.— The levator scapulæ ventralis of placentals may well be homologous with the ventral part of the omotrachelian of monotremes since the origins and insertions are similar in placentals and *Echidna* (see Westling, 1889, p. 13). The origin on the atlantal hypapophysis in *Ornithorhynchus* is doubtless secondary. In *Thylacinus* the muscle is broader than in placentals and has the same insertion as in the latter group.

It appears that the omotrachelian, being a superficial layer, was carried up on the acromion when the latter was everted, leaving the levator ventralis behind to become crowded out upon the advent of the supraspinatus. In *Echidna* the supraspinatus is larger than in *Ornithorhynchus* and the levator ventralis is correspondingly absent.

Levator scapulæ

CARNIVORA (Windle and Parsons, 1897, pp. 388–389)

Levator scapulæ dorsalis (= occipitoscapularis)

Origin.— Posterior tubercles of cervical transverse processes.

Insertion.— Vertebral part of subscapular fossa (with serratus anterior).

Innervation.— (Man) Nn. cervicales III, IV, V.

ORNITHORHYNCHUS (McKay, 1894, pp. 338–339)

Levator scapulæ dorsalis (Pls. XLII, *lev. scap. dors.*)

Origin.— Tips of transverse processes of cervicals 2–7.

Insertion.— Posterior half of inner edge of vertebral border of scapula.

Levator scapulæ ventralis (Pls. XLII, *lev. scap. vent.*)

Origin.— Transverse processes of cervicals 2–6.

Insertion.— Inner half of vertebral border of scapula and whole length of anterior costa and that portion of the supraspinous fossa lying between the insertion of the ventral part of the omotrachelian (ventral portion) and the true anterior costa (median ridge on antero-internal surface).

Innervation.— Nn. cervicales III, IV, V, and VI.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, *lev. scap.*; XL)

Dorsal portion

Origin.—Transverse processes of cervical vertebræ.

Insertion.—Dorsal edge of inner surface and the whole anterior border of the suprascapula.

Ventral portion

Origin.—Transverse processes of cervical vertebræ.

Insertion.—Median half of anterior border of spine medial to insertion of the omotrachelian, as in monotremes.

SPHENODON (Fürbringer, 1900, pp. 467–468)

Levator scapulæ profundus (Fig. 2, A^1 , A^2 , *lsprf.*)

“Outer” portion

Origin.—Tips of ribs of fifth, sixth, and seventh vertebræ.

Insertion.—Inner surface of cartilaginous suprascapula.

“Inner” portion

Origin.—Transverse processes of third to eighth vertebræ.

Insertion.—Inner surface of cartilaginous suprascapula, dorsal to “outer” portion.

Innervation.—Spinal nerves IV, V, VI, VII, and VIII.

Remarks.—The two divisions of the levator scapulæ profundus of *Sphenodon* probably do not correspond with the two divisions in *Ornithorhynchus*.

In *Cynognathus* the muscle is here placed as in *Ornithorhynchus* because of the presence of the scapular spine and the exclusion of the supraspinatus from its usual position. The ventral portion of the true levator is absent in *Echidna*.

Serratus anterior

CARNIVORA (Windle and Parsons, 1897, pp. 388–389)

Origin.—First to tenth thoracic ribs.

Insertion.—Vertebral part of subscapular fossa (with levator scapulæ dorsalis).

Innervation.—“Posterior thoracic or nerve of Bell.”

ORNITHORHYNCHUS (McKay, 1894, p. 339) (Pl. XLII, *serr. ant.*)

Origin.—First to third dorsal ribs, midway between vertebræ and sternum.

Insertion.—Inside surface of suprascapula and scapula below the insertion of the levator scapulæ dorsalis and above the subscapularis.

Innervation.—(*Ornithorhynchus*) Nn. cervicales III, IV, V, VI.

CYNOGNATHUS (inferred conditions)

Serratus superficialis (Pls. XXXIX, *serr. supf.*; XL, XLI)

Origin.—As in Crocodile.

Insertions.—Flattened posterior border of scapula as far as tubercle for insertion of triceps.

Serratus profundus (Pls. XXXIX, *serr. ant.*; XL, XLI)Origin.—As in *Sphenodon* and perhaps extending further forward.

Insertion.—Inside surface of suprascapula and scapula below the insertion of the dorsal portion of the levator scapulæ and dorsal to the subscapularis.

CROCODILE (Fürbringer, 1876, pp. 776–778; 1900, p. 501)

Serratus superficialis (= thoraci-scapularis superficialis) (Fig. 4, *thssp.*)

Origin.—Last cervical and first three dorsal ribs.

Insertion.—Nearly all of hinder border of scapula.

Innervation.—Nn. thoracici superiores VIII and IX.

Serratus profundus

Origin.—From transverse process of fifth cervical vertebra to first or second rib.

Insertion.—Ventral part of inner surface of suprascapula and adjacent part of scapula.

Innervation.—Nn. thoracici superiores VI–IX.

SPHENODON (Fürbringer, 1900, pp. 466–468)

Serratus superficialis (Fig. 2, *sspf.*)

Origin.—Ribs of eighth and ninth vertebræ.

Insertion.—Postero-ventral moiety of inner border of suprascapula and small adjacent part of scapula.

Innervation.—N. thoracalis superioris (= branch of N. spinalis VIII); also may receive branches from Nn. VII and VIII, or VIII and IX.

Serratus profundus

Upper part

Origin.—Ends of the ribs of fifth, sixth and seventh vertebræ.

Insertion.—Anterior two-thirds of suprascapula, along the middle of the inner face.

Lower part

Origin.—Ribs of last five or six cervical vertebræ.

Insertion.—Five-sixths of the entire width of suprascapula above the insertion of the serratus profundus (upper part) and with the levator scapulæ dorsalis.

Innervation.—N. thoracalis superioris from N. spinales IV or V–VIII.

Omohyoid

CARNIVORA (Windle and Parsons, 1897, pp. 379–380)

Origin.—Hyoid bone.

Insertion.—Anterior border of scapula near suprascapula notch.

Innervation.—(Man) Ansa hypoglossi.

ORNITHORHYNCHUS (McKay, 1894, pp. 345–346) (Pl. XLII, *omohy.*)

Origin.—Basihyal and tendinous intersection of mylo- and stylohyoid.

Insertion.—Inner surface of scapula on a small area between the origin of the supraspinatus and the ventral extremity of the median internal ridge (“true anterior costa”).

Innervation.—N. hypoglossus (?).

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLII)

Origin.—Hyoid bone.

Insertion.—A facet on dorsal surface of medial acromial ridge, beneath clavicle.

SPHENODON (Osawa, 1898, pp. 525, 540) (Fig. 1, *A*², *ohy.*)

Origin.—Hyoid bone.

Insertion.—Inner surface of scapula near acromion and on sternoscapular ligament.

Innervation.—N. hypoglossus and N. cervicalis I, ramus ventralis.

Remark.—The omohyoid seems to be strictly homologous in reptiles and mammals.

Origins, Insertions, and Innervations of Muscles Arising on the Scapulo-coracoid and Clavicle in Recent Placentals, Monotremes and Reptiles, with Inferred Conditions in *Cynognathus*

Deltoideus

CARNIVORA (Windle and Parsons, 1897, p. 389)

Spino-deltoideus

Origin.—Spine of scapula.

Insertion.—Deltoid crest, dorsal to and beneath the acromio-deltoideus.

Acromio-deltoideus

Origin.—Posterior side of acromion.

Insertion.—Deltoid crest.

Clavo-deltoideus

Origin.—Clavicle on clavicular ligament.

Insertion.— Lower half of front face of humerus and sometimes on forearm.

Innervation.— (Cat) N. axillaris.

ORNITHORHYNCHUS (McKay, 1894, pp. 281–282)

Spino-deltoides (= “scapular portion”) (Pl. XLI)

Origin.— Anterior two-fifths of external edge of vertebral border of scapula and adjoining external surface; and from upper one-third of outer border of spine.

Insertion.— Tubercle at about mid-point of deltoid crest.

Innervation.— N. axillaris.

Acromio-clavo-deltoides (= “acromio-clavicular part”) (Pl. XLI)

Origin.— Ventral surface of transverse portion of interclavicle and the acromion.

Insertion.— Distal three-fourths of deltoid crest and adjoining posterior face of humerus.

Innervation.— N. axillaris and possibly also a minute twig from N. supracoracoideus.

CYNOGNATHUS (inferred conditions)

Probably about as in monotremes (Pls. XXXIX, XL, XLI)

SPHENODON (Fürbringer, 1900, pp. 482–486)

Deltoides scapularis (= spino-deltoid + teres minor = dorsalis scapulæ) (Fig. 1, A^2 , *dsc.*)

Origin.— Anterior three-fourths and ventral two-thirds of outer face of suprascapula and the adjoining edge of scapula.

Insertion.— Greater tuberosity (processus lateralis, or deltoid crest) of humerus.

Deltoides clavicularis (= clavo + acromio-deltoides = cleido-humeralis) (Fig. 1, A^2 , *dc.*)

Origin.— Clavicle and interclavicle.

Insertion.— Greater tuberosity (processus lateralis) of humerus.

Innervation.— N. axillaris, ramus cleido-humeralis of ramus dorsalis scapulæ.

Teres minor

CAT (Reighard and Jennings, 1902, p. 161)

Origin.— Glenoid border of scapula.

Insertion.— Greater tuberosity of humerus.

Innervation.— (Man) N. axillaris.

ORNITHORHYNCHUS (McKay, 1894, pp. 316–317) (Pl. XLI.)

Origin.— External face of scapula on ridge extending from dorso-anterior border of glenoid cavity posteriorly and dorsally to the

glenoid crest at the junction of its upper two-thirds with its ventral one-third.

Insertions.—Posterior border of ventral aspect of lesser tuberosity.

Innervation.—A cord formed from fourth, fifth, and sixth cervicals and (in *Echidna*) from the N. axillaris as well.

CYNOGNATHUS (inferred conditions) (Pls. XL, XLI)

Origin.—Possibly from a depression on the posterior surface of the scapula lying between the tuberosity for the tendon of the triceps and the glenoid crest.

Insertions.—Dorsal (posterior) face of humerus lateral to the tuberosity for the insertion of latissimus dorsi and teres major.

SPHENODON

[See under *deltoideus*, above.]

Teres major

CARNIVORA (Windle and Parsons, 1897, pp. 390–391)

Origin.—Dorsal third of axillary border of scapula.

Insertion.—Anterior surface of tendon of M. latissimus dorsi.

Innervation.—(Cat) middle subscapular nerve.

ORNITHORHYNCHUS (McKay, 1894, pp. 314–315) (Pl. XLI)

Origin.—Posterior third of external margin of vertebral border and immediately adjoining face of scapula.

Insertion.—Middle third of inner border of humerus distal to insertion of subscapularis on lesser tuberosity.

Innervation.—Nn. cervicales IV, V, and VI “from which the subscapular nerves also spring.”

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, *ter. maj.*; XL)

Origin.—Dorsal fourth of inner part of axillary border of scapula.

Insertion.—Dorso-posterior surface of humerus on tuberosity for tendon of this muscle and the latissimus dorsi.

SPHENODON

The teres major may be represented either by the anterior part of the latissimus dorsi or possibly by the scapulo-humeralis posterior (see p. 473 below).

Subscapularis

CARNIVORA (Windle and Parsons, 1897, p. 390)

Origin.—Nearly all of internal face of scapula ventral to insertion of serratus anterior and sometimes also from the axillary border.

Insertion.—Lesser tuberosity of humerus.

Innervation.—(Cat) cranial branch of subscapular nerve.

ORNITHORHYNCHUS (McKay, 1894, pp. 314-315) (Pl. XLI)

Origin.— Extensive area on both external and internal faces of scapula.

Insertion.— Distal extremity of lesser tuberosity of humerus.

Innervation.— N. subscapularis from Nn. cervicales IV, V, and VI.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLI, XLII)

Origin.— Nearly entire inner, triangular surface of scapula below insertion of serratus anterior.

Insertion.— Lesser tuberosity (processus medialis).

SPHENODON (Fürbringer, 1900, pp. 489-490)

Pars scapularis of subcoraco-scapularis (= subscapularis).

Origin.— Hinder edge of scapula beneath sterno-scapular ligament.

Insertion.— Lesser tuberosity (processus medialis).

Innervation.— N. subcoraco-scapularis.

SubcoracoideusPRIMATES (*Cercopithecus*)

(= coracobrachialis brevis)

Origin.— Ventral surface of coracoid process internal to insertions of biceps brachii and coracobrachialis.

Insertion.— Medial surface of humerus between lesser tuberosity and insertion of teres major. [Occurs in man as a variant.]

Innervation.— (?)

CARNIVORA (Windle and Parsons, 1897, pp. 392-393)

(= rotator humeri, or coracobrachialis brevis)

Origin.— Minute coracoid process.

Insertion.— "Surgical neck" of humerus after "having passed above [over the cephalic border of] the latissimus dorsi."

Innervation.— (?)

ORNITHORHYNCHUS (McKay, 1894, pp. 289-299) (Pl. XLII)

(= epicoraco-brachialis)

Origin.— Outer half of dorsal surface of epicoracoid and adjoining surface of coracoid.

Insertion.— Lesser tuberosity near insertion of subscapularis.

Innervation.— N. musculo-cutaneous and from cord from Nn. cervicales IV, V, and VI.

CYNOGNATHUS (inferred conditions) (Pls. XL, XLI, XLII)

Origin.— Dorsal inner surface of epicoracoid and adjacent surface of scapula.

Insertion.— Lesser tuberosity (processus medialis).

SPHENODON (Fürbringer, 1900, pp. 489–490)

(= pars coracoideus of subcoraco-scapularis)

Origin.—Three-fifths of inner surface of epicoraco-coracoid and scapula.

Insertion.—Lesser tuberosity (processus medialis) with pars scapularis.

Innervation.—N. subcoracoscapularis.

Infraspinatus

CARNIVORA

Origin.—Whole infraspinous fossa except small ventral part of same.

Insertion.—Greater tuberosity of humerus.

Innervation.—N. suprascapularis.

ORNITHORHYNCHUS (McKay, 1894, pp. 305–306) (Pl. XLI)

Origin.—Large part of anterior three-fourths of lateral surface of scapula.

Insertion.—Inner part of ventral surface of greater tuberosity and small area on posterior surface of humerus immediately internal to the proximal end of the delto-pectoral ridge.

Innervation.—Chiefly from the N. suprascapularis and in part from the N. axillaris; (Echidna) same.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLI)

Origin.—Nearly whole of infraspinous fossa.

Insertion.—Greater tuberosity (processus lateralis).

SPHENODON (Fürbringer, 1900, pp. 486–489)

Possibly a part of the epicoraco-humeralis, or possibly represented by the following muscle:

Scapulo-humeralis

Scapulo-humeralis anterior (Fig. 2, *A*¹, *scha.*)

Origin.—Dorsal, outer border of coracoid and ventral edge of scapula above M. epicoraco-humeralis.

Insertion.—Fossa between deltoid crest and greater tuberosity.

Innervation.—N. scapulo-humeralis, ramus anterior [= branch of N. axillaris].

Scapulo-humeralis posterior (Fig. 2, *A*¹, *schp.*)

Origin.—Outer surface of anterior three-fourths of ventral half of scapula.

Insertion.—Dorsal surface of humerus near and medial to insertion of scapulo-humeralis anterior.

Innervation.—N. scapulo-humeralis, ramus posterior [= branch of N. axillaris].

Supraspinatus

CARNIVORA

Origin.—Whole of supraspinous fossa except small ventral area.

Insertion.—Greater tuberosity.

Innervation.—N. suprascapularis.

ORNITHORHYNCHUS (McKay, 1897, pp. 308–309) (Pls. XLI, XLII)

Origin.—Internal face of scapula from a depression between acromion and glenoid cavity near sharp antero-ventral border of scapula.

Insertion.—Ventral aspect of inner part of greater tuberosity.

Innervation.—N. supracoracoideus.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLI, XLII)

Origin.—Roughened pit on the ventro-median side of the acromial ridge.

Insertion.—Greater tuberosity and part of fossa distal to latter.

SPHENODON

Absent, or not differentiated, probably part of the epicoraco-humeralis (Pl. XLIX)

Epicoraco-humeralis (= supracoracoideus)

PLACENTALS

Absent.

ORNITHORHYNCHUS (McKay, 1894, pp. 287–288) (Pls. XLI, XLII, XLIX)

Origin.—Nearly entire ventral surface of epicoracoid.

Insertion.—Ventral surface of greater tuberosity.

Innervation.—N. supracoracoideus.

Remarks.—Evidently the suprascapular nerve of placentals is a branch of the supracoracoideus.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL)

Origin.—Ventral surface of epicoracoid and precoracoid surrounding the foramen supracoracoideum.

Insertion.—Greater tuberosity (processus lateralis).

SPHENODON (Fürbringer, 1900, pp. 474–475) (Pl. XLIX)

Supracoracoideus (Fig. 1, *A*² *spc.*)

Origin.—Anterior half of epicoraco-coracoid.

Insertion.—Greater tuberosity (processus lateralis) and lateral scapulo-humeral ligament.

Innervation.—N. supracoracoideus.

Coracobrachialis

PRIMATES

Coracobrachialis medius

Origin.— Tip of coracoid process.

Insertion.— Middle of humerus along medial side.

Innervation.— N. musculocutaneus.

Coracobrachialis longus

Origin.— Tip of coracoid process.

Insertion.— Distal third of humerus along medial side. [Occurs in man as a variant.]

Innervation.— (?)

ORNITHORHYNCHUS (McKay, 1894, pp. 298–301)

Coracobrachialis medius (= “coracobrachialis brevis” of McKay) (Pls. XLII, XLIX)

Origin.— Concave and outer, posterior border of coracoid between glenoid and origin of coracobrachialis longus. Also from ventral face of coracoid.

Insertion.— Antero-lateral face of humerus on distal curved ridge from greater to lesser tuberosity. Insertion bordered internally by the epicoracobrachialis and teres major, externally and distally by the posterior part of the latissimus dorsi.

Innervation.— Division of musculocutaneous nerve.

Coracobrachialis longus (Pls. XLII, XLIX)

Origin.— By tendon with coracoid head of biceps from the external portion of the distal extremity of the coracoid.

Insertion.— Ridge above entepicondylar foramen.

Innervation.— N. musculocutaneus.

CYNOGNATHUS (inferred conditions)

Coracobrachialis medius et longus (Pls. XLI, XLII)

Origin.— Distal tip of coracoid.

Insertion.— As in *Ornithorhynchus*.

SPHENODON (Fürbringer, 1900, pp. 475–477)

Coracobrachialis medius (= “brevis” of Fürbringer) (Fig. 3, A^2 , *cbrb.*)

Origin.— Outer (ventral surface of posterior half of epicoraco-coracoid.

Insertion.— Concavity of ventral surface of proximal end of humerus between the greater and lesser tuberosities.

Innervation.— Nn. coracobrachialis, rami proximalis et distalis.

Coracobrachialis longus (Fig. 3, A^1 , A^2 , *cbrl.*)

Origin.— Outer surface of posterior tip of epicoraco-coracoid.

Insertion.—Medio-distal surface of humerus just proximal to entepicondylar foramen.

Innervation.—Same as for coracobrachialis medius.

Biceps brachii

PRIMATES

Long head

Origin.—Supraglenoid tuberosity [= “subcoracoid process”].

Short head

Origin.—Tip of coracoid process.

Insertion.—Dorsal half of bicipital tuberosity of radius, with long head.

Innervation.—N. musculocutaneus (two branches).

ORNITHORHYNCHUS (McKay, 1894, pp. 295–297)

Epicoracoid head (Pls. XLI, XLII, XLIX)

Origin.—Small area on posterointernal portion of ventral surface of epicoracoid.

Insertion.—With coracoid head.

Coracoid head (Pls. XLI, XLII, XLIX)

Origin.—External border of distal extremity of coracoid, with coracobrachialis longus.

Insertion.—Middle third of ulna.

Innervation.—N. musculocutaneus from Nn. cervicales IV, V, VI, and VII.

CYNOGNATHUS (inferred conditions) (Pls. XXXIX, XL, XLI, XLII)

Origin.—Ventral surface of coracoid and possibly also in part from the epicoracoid.

Insertion.—As in *Ornithorhynchus*.

SPHENODON (Fürbringer, 1900, pp. 477–479)

Anterior portion (Fig. 1, A^2 , $bi.$; Fig. 3, A^2 ; Pl. XLIX)

Origin.—Sagittal, middle third of outer surface of coracoid.

Insertion.—Proximal part of radius and ulna.

Posterior portion (Fig. 1, A^2 , bi_{11} ; Fig. 3, A^2 ; Pl. XLIX)

Origin.—A fine strip of muscle from the posterior border of the coracoid with the coracobrachialis longus.

Insertion.—With anterior portion.

Innervation.—Nn. bicipitalis proximalis and bicipitalis distalis.

Homologies of Muscles of the Shoulder-girdle in Reptiles and Mammals, with Inferred Conditions in *Cynognathus*.

Innervation from	SPHENODON (Fürbringer)	CROCODYLIA (Fürbringer)	CYNOGNATHUS (inferred)	MONOTREMES (McKay)	PLACENTALS (Windle and Parsons)
<i>N. accessorius</i>	Trapezius	Trapezius	Anterior trapezius Posterior trapezius	Anterior trapezius Posterior trapezius	Cleidomastoideus Sternomastoideus Clavotrapezius Acromiotrapezius Spinotrapezius
	Omohyoideus	Omohyoideus	Omohyoideus	?	Omohyoideus
<i>N. hypoglossus</i> + <i>N. c 1</i>	Levator scapulæ superior	Levator scapulæ superficialis	Omotrachelius dorsalis	Omotrachelius dorsalis	Absent
	Levator scapulæ inferior		Omotrachelius ventralis	Omotrachelius ventralis	Omotrachelius (= Levator scapulæ ventralis)
<i>Nn. cervicales</i> 4 to 8	Levator scapulæ profundus	Levator scapulæ profundus	Levator scapulæ dorsalis	Levator scapulæ dorsalis	Levator scapulæ dorsalis
			Levator scapulæ ventralis	Levator scapulæ ventralis	Absent
			Rhomboideus?	Rhomboideus	Rhomboideus
		<i>N. 2</i> Rhomboideus		<i>N. 3</i>	4, 5, or 6
				3 to 6	3 to 5 (<i>man</i>)
				<i>N. 3</i>	<i>N. 3</i> (cat)
					<i>Ansa hypoglossi</i>

Innervation from	SPHENODON (Fürbringer)	CROCODYLIA (Fürbringer)	CYNOGNATHUS (inferred)	MONOTREMES (McKay)	PLACENTALS (Windle and Parsons)
<i>N. thorac. sup.</i> (<i>Nn.</i> 4 or 5 <i>N.</i> <i>Nn.</i> 7+8 or 8+9)	Pectoralis	Pectoralis	Pectoralis	Pectoralis	Pectoralis
	Serratus superficialis Serratus anterior profundus	Serratus superficialis Serratus anterior profundus <i>N.</i> 6 to 9	Serratus superficialis Serratus anterior profundus	Absent <i>N.</i> 3-6 Serratus anterior	Absent <i>N. thor. post.</i> Serratus anterior
<i>N. suprascapularis</i> (<i>N. supracoracoideus</i>)	Epicoraco-humeralis (in part)	Pars coracoidea of supracoracoideus Pars scapularis of supracoracoideus	Epicoraco-humeralis Supraspinatus	Epicoraco-humeralis Supraspinatus <i>N. supracoracoideus</i>	Absent <i>N. suprascap.</i> Supraspinatus
		Scapulo-humeralis (ant.+post.)	Infraspinatus	<i>N. suprascap.</i> <i>N. axil.</i> Infraspinatus	Infraspinatus

Innervation from	SPHENODON (Fürbringer)	CROCODILLA (Fürbringer)	CYNOGNATHUS (inferred)	MONOTREMES (McKay)	PLACENTALS (Windle and Parsons)
Nn. subscapulares	Subscapularis (pars coracoideus) (pars scapularis) Latissimus dorsi	Subscapularis Teres major Latissimus dorsi	Subcoracoideus Subscapularis Teres major Latissimus dorsi	Subcoracoideus (= epicor. brach.) Subscapularis Teres major Latissimus dorsi	Subcoracoideus (= coraco-brach. brevis) Subscapularis Teres major Latissimus dorsi
	Scapulo-deltoid Clavo-deltoid	Scapulo-deltoid (= dorsalis scapulæ) Deltoides scapularis inferior	Teres minor Spino-deltoid Clavo-deltoid	N. 4 to 6 + N. axil. Teres minor Spino-deltoid Clavo-deltoid	N. axillaris Teres minor Spino-deltoid Acromio-deltoid Clavo-deltoid
N. musculo-cut. (N. cor. brach., N. bicip.)	Biceps brachii Coracobrachialis medius ("brevis" Fürb.) Coracobrachialis longus	Biceps brachii Coracobrachialis	Biceps brachii Coracobrachialis medius Coracobrachialis longus	Biceps brachii Coracobrachialis medius Coracobrachialis longus	Biceps brachii Coracobrachialis medius Coracobrachialis longus
	Triceps	Triceps	Triceps	Triceps	Triceps
N. radialis					

REVIEW AND IDENTIFICATION OF MUSCLES CONNECTED WITH THE PELVIS
AND SACRUM IN PLACENTALS, MONOTREMES, SPHENODON, AND OTHER
REPTILES, WITH INFERRED CONDITIONS IN CYNOGNATHUS

By W. K. Gregory and C. L. Camp

The following simple classification of these muscles may make it easier to remember the correspondence of reptilian (listed below on the right) to mammalian (on the left) muscles, and may prepare the way for a discussion of the functions of the muscles.

A.—Muscles Chiefly in Front of the Pelvis

Sacrospinalis	Ilio-costalis cervicis
Longissimus dorsi	
Ilio-costalis	
Obliquus abdominis externus	Obliquus abdominis externus
Rectus abdominis	Rectus abdominis
Pyramidalis	Part of abdominal muscles
Quadratus lumborum }	Quadratus lumborum
Psoas minor }	
Iliacus }	Pubi-ischio-femoralis (trochantericus)
Psoas major }	internus
Pectineus }	

B.—Superficial Muscles of the Thigh and Knee

Rectus femoris	Ambiens
Quadriceps femoris	Femoro-tibialis
Sartorius	Ilio-tibialis internus
	(Ilio-tibialis II)
Gluteus maximus }	Extensor ilio-tibialis
Agitator caudæ }	(Ilio-tibialis I)
Biceps }	Ilio-fibularis
Tenuissimus }	
Semitendinosus	Flexor tibialis externus
Semimembranosus	Flexor tibialis internus

C.—Muscles on the Inner Side of the Thigh (Adductors, etc.)

Gracilis	Pubi-ischio-tibialis
Adductor longus }	Pubi-ischio-femoralis
Adductor brevis }	
Adductor magnus }	

Obturator externus	Pubi-ischio-femoralis externus
Quadratus femoris	Pubi-ischio-femoralis posterior
Gemellus inferior (?)	
Obturator internus	

D.—Deep Gluteal and Tail Muscles

Tensor fasciæ femoris	Ilio-femoralis
Gluteus medius	
Gluteus minimus	
Gluteus ventralis	
Gluteus profundus	
Pyriformis	Caudi-ilio-femoralis
Gemellus superior	
Caudi-femoralis	Caudi-femoralis (partim)
Extensor caudæ medialis	Musculus caudæ dorsalis (partim)
Extensor caudæ lateralis	
Abductor caudæ externus	Ilio-caudalis
Ischio-coccygeus	Ischio-caudalis
Levator ani	"Aftermuskeln"
Pubo-rectalis	(Partly derived from ischio-caudalis.
Pubo-coccygeus	Gadow)
Ilio-coccygeus	
Ilio-sacralis	
Flexor caudæ longus	?Caudi-femoralis (partim)

A.—Muscles Chiefly in Front of the Pelvis

Sacrospinalis

CAT (Reighard and Jennings, 1902, pp. 126–128)

Longissimus dorsi

Origin.—Crest and medial surface of ilium, caudal to articular impression, also from deep layer of lumbo-dorsal fascia.

Insertion.—Transverse processes of thoracic vertebræ.

Innervation.—Dorsal rami of thoracic nerves.

Ilio-costalis (lateral part of the sacrospinalis)

Origin.—By many partly separated bundles lying above the ribs, lateral to the longissimus dorsi.

Insertion.—By tendons on the lateral surface of the ribs.

ORNITHORHYNCHUS (Coues, 1870, pp. 133–134)

"*Sacrolumbalis*"

Origin.—Anterior tip of ilium.

Insertion.—Ribs and transverse processes of cervical vertebræ.

CYNOGNATHUS (inferred conditions) (Pl. XLIV)

Origin.—Medial side of dorsal border of ilium and dorsal surfaces of sacral vertebræ.

Insertion.—Dorsal surfaces of transverse processes and ribs, of lumbar and thoracic vertebræ.

SPHENODON (Osawa, 1898, p. 542)

Ilio-costalis cervicis (Pl. XLIII)

Origin.—Anterior border of ilium and dorsal surface of lumbar, sacral and caudal vertebræ?

Insertion.—Ends of transverse processes and dorsal and outer surfaces of cervical ribs.

Innervation.—R. dorsales of N. spinales.

Obliquus abdominis externus

CAT (Reighard and Jennings, 1902, pp. 153–154)

Origin.—Posterior nine or ten ribs.

Insertion.—Median raphe and linea alba, tubercle and cranial border of pubis.

Innervation.—R. ventrales of Nn. thoracales posteriores.

ECHIDNA (Mivart, 1866, p. 381)

Origin.—All ribs except first, and the ilium.

Insertion.—Anterior border of symphysis pubis and internal and external margins of the marsupial bone, and margin of pubis just external to base of marsupial bone.

Innervation.—(?)

CYNOGNATHUS (inferred conditions) (Pls. XLIV, XLV)

Origin.—Posterior ribs.

Insertion.—Marsupial bone and pubis nearby.

SPHENODON (Osawa, 1898, pp. 544, 626) (Pl. XLIII)

Origin.—Uncinate processes of ribs.

Insertion.—Anterior surface of M. rectus abdominis, also on tuberculum pubis and ligamentum postischadicum.

Innervation.—Nn. thoracales.

Rectus abdominis

CAT (Reighard and Jennings, 1902, pp. 155–156)

Origin.—Tuberculum pubis.

Insertion.—First and second costal cartilages and sternum between first and fourth cartilages.

Innervation.—R. ventrales of Nn. thoracales and lumbales I–III.

ECHIDNA (Mivart, 1866, p. 382)

Origin.— Deep surface of marsupial bone near its external margin.

Insertion.— Posterior end of sternum.

Innervation.— (?)

CYNOGNATHUS (inferred condition)

Origin.— Marsupial bone (Pl. XLIV)

Insertion.— Along sternum.

SPHENODON (Osawa, 1898, pp. 547–548, 626) (Pl. XLIII)

Origin.— Tuberculum pubis and ventral surface of pubis and ischium.

Insertion.— Caudal border of sternum.

Innervation.— Nn. intercostales from nervi thoracales.

Pyramidalis

CAT (absent, according to Reighard and Jennings)

UNGULATA (absent, according to Windle and Parsons)

MAN (often absent)

Origin.— Pubic crest in front of rectus abdominis.

Insertion.— Linea alba.

ECHIDNA (Mivart, 1866, p. 382)

Origin.— Whole inner surface of marsupial bone.

Insertion.— Whole length of linea alba.

Innervation.— (?)

CYNOGNATHUS (inferred condition).

Origin.— Marsupial bone.

Insertion.— Linea alba.

SPHENODON (Osawa, 1898; Gadow, 1882, pp. 94, 95).

Not differentiated from rectus abdominis.

Quadratus lumborum**UNGULATA** (Windle and Parsons, 1903, p. 289)

Origin.— Ventral surfaces of transverse processes of lumbar vertebræ, and usually into heads of several posterior ribs.

Insertion.— Sacro-iliac joint on tubercle nearby on ilium.

Innervation.— (Reighard and Jennings, 1902, p. 394). Ventral rami of second and third lumbar nerves (cat).

ECHIDNA (Mivart, 1866, p. 390)

Origin.— Ventral surfaces and posterior margins of posterior two ribs, also sides of centra and transverse processes of the three lumbar vertebræ.

Insertion.— Anterior margin of ilium.

Innervation.— (Westling, 1889, p. 52) Plexus lumbalis.

CYNOGNATHUS (inferred conditions) (Pl. XLIV)

Origin.—Ventral surfaces of dorsal vertebræ and posterior ribs.

Insertion.—Sacro-iliac joint.

SPHENODON (Osawa, 1898, p. 548)

Origin.—Anterior borders of transverse processes of sacral vertebræ (metameric) inward and forward.

Insertion.—Anterolateral surfaces of five presacral vertebræ.

Innervation.—(Gadow, 1882, (b), p. 70), N. spinales 19–24 (alligator).

Remarks.—According to Gadow (1882, pp. 71 and 418) the quadratus lumborum of reptiles includes both the quadratus lumborum and the psoas [minor] of man, and is serially homologous on the one hand with the intercostal muscles and on the other hand with the pubischiofemoralis internus (Part III). In the Crocodilia this powerful muscle is attached to the femur, in front of the great trochanter; it draws the femur forward, inward and upward.

Psoas minor

UNGULATA (Windle and Parsons, 1903, p. 289)

Origin.—Iliopectineal eminence.

Insertion.—Centra of last three or four thoracic and several of the lumbar vertebræ.

Innervation.—(Reighard and Jennings, 1902, p. 394). Rami ventrales of Nn. lumbales II et III (cat).

ECHIDNA (Mivart, 1866, pp. 389–390)

Origin.—Iliopectineal eminence posterior to origin of sartorius.

Insertion.—Last three ribs and centra of last three dorsal vertebræ.

Innervation.—(Westling, 1889, p. 52). Plexus lumbalis.

CYNOGNATHUS (inferred condition)

Perhaps not yet differentiated from *quadratus lumborum*.

SPHENODON

Not differentiated from *quadratus lumborum*.

Iliacus

UNGULATA (Windle and Parsons, 1903, p. 289)

Origin.—Iliac fossa, ventral sacrosciatic ligament, and margin of sacrum.

Insertion.—Lesser trochanter.

Innervation.—(Reighard and Jennings, 1902, p. 397). N. femoralis (cat).

ECHIDNA (Mivart, 1866, p. 390)

Origin.—Whole ventral surface of ilium.

Insertion.—Lesser trochanter and ridge running distally therefrom.

Innervation.—(Westling, 1889, p. 53). N. femoralis.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—Inner surface of pubis and ischium.

Insertion.—Region of lesser trochanter.

SPHENODON (Osawa, 1898, pp. 571–572)

Pubi-ischio-femoralis internus (Partim) (Pls. XLIII, XLV)

Origin.—Inner surfaces of pubis, ischium and membrana obturatoria; over anterior pubi-iliac angle to

Insertion.—Forward medial surface of proximal part of femur.

Innervation.—Nn. iliopectinei from plexus cruralis.

Psoas major

UNGULATA (Windle and Parsons, 1903, p. 289)

Origin.—Transverse processes and sides of centra of all lumbar vertebræ and centra of posterior thoracic vertebræ.

Insertion.—Lesser trochanter.

Innervation.—(Cat) (Reighard and Jennings, 1902, p. 397). Ventral rami of lumbar nerves V and VI (N. femoralis).

ECHIDNA (Mivart, 1866, p. 390)

Origin.—The three lumbar and first three sacral vertebræ.

Insertion.—Lesser trochanter.

Innervation.—(Westling, 1889, p. 53). N. femoralis.

CYNOGNATHUS (inferred condition).

Part of iliacus (Pl. XLV)

SPHENODON

Part of *pubi-ischio-femoralis internus* (Pls. XLIII, XLV)

Pectineus

UNGULATA (Windle and Parsons, 1903, pp. 272–273)

Origin.—Whole iliopectineal line.

Insertion.—Variable, middle third of femur in *Hyrax*.

Innervation.—Femoral or obturator nerve or both.

ECHIDNA (Westling, 1889, p. 34)

Origin.—Iliopectineal eminence.

Insertion.—Border of femur distal to lesser trochanter.

Innervation.—Branch of N. femoralis (to this muscle and the sartorius).

CYNOGNATHUS (inferred condition)

Origin.— Iliopectineal eminence.

Insertion.— Medial side of femur.

SPHENODON

Part of *pubi-ischio-femoralis internus* (Pl. XLIII)

Remarks.— The pubi-ischio-femoralis internus of reptiles has much of the position and functions of the ilio-psoas + pectineus of mammals, except that it extends further caudad on the inner side of the pelvis.

B.— Superficial Muscles of the Thigh and Knee

Rectus femoris

CAT (Reighard and Jennings, 1902, p. 201)

Origin.— Triangular area on ilium above acetabulum between acetabular and ischial borders.

Insertion.— Outer surface of patella near proximal border of same.

Innervation.— Ventral rami of sixth and seventh lumbar nerves (N. femoralis).

ORNITHORHYNCHUS (Coues, 1868, p. 166)

Origin.— Iliac shaft just above and anterior to acetabulum (Pl. XLV).

Insertion.— Patella, and, by a second division, into head of tibia.

Innervation.— (Westling, 1884, p. 39). N. femoralis.

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.— Tuberculum pubis.

Insertion.— Head of tibia.

SPHENODON (Osawa, 1898, p. 576, and Gadow, 1882, pp. 375–377) (Pls. XLIII, XLV)

Ambiens = "*pubo-tibialis*"

Origin.— Near base of tuberculum pubis.

Insertion.— With tendon of femoro-tibialis on anterior surface of caput tibiae.

Innervation.— R. pubi-tibialis of N. femoralis.

Sartorius

ARTIODACTYLA (Windle and Parsons, 1903, p. 275)

Origin.— (Bovidæ) from iliac fascia and Poupart's ligament and by another head from pubis just internal to femoral vessels.

Insertion.— Upper part of tibia on fascia of thigh or on tendon of gracilis.

Innervation.— N. femoralis (ant. crural).

ECHIDNA (Westling, 1889, p. 34)

Origin.—Iliopectineal process.

Insertion.—Median side of capsule of knee over tibia and beneath gracilis.

Innervation.—Branch of N. femoralis (to this muscle and the pectineus).

CYNOGNATHUS (inferred condition) (Pl. XLV)

Ilio-tibialis internus

Origin.—Iliopectineal process.

Insertion.—Inside of head of tibia beneath gracilis.

SPHENODON (Gadow, 1882 (b), pp. 408–410, and Osawa, 1898, p. 575)

Pubi-tibialis (posticus) (Pls. XLIII, XLV)

Origin.—Tubercle of pubis.

Insertion.—Latero-proximal (= medio-proximal) prominence of tibia.

Innervation.—R. pubi-tibialis of N. obturatorius and Rr. breves of N. femoralis.

Remarks.—According to Gadow's later view (1891, p. 150) the pubi-tibialis of lizards (and *Sphenodon*) is not homologous with the sartorius of mammals. The latter is innervated by the anterior crural nerve, which also supplies the quadriceps extensor, psoas, iliacus, and pectineus. In the alligator the ilio-tibialis internus (ilio-tibialis II) is likewise innervated by twigs from the anterior crural nerve, which supplies the homologues of the other muscles named above. We, therefore, provisionally adopt the view that the sartorius of mammals has been derived from the ilio-tibialis internus, which may have been present in primitive reptiles.

Gluteus maximus

PERISSODACTYLA (Windle and Parsons, 1903, pp. 264–266)

(= *Ectogluteus*)

Origin.—Spines of sacral and anterior caudal vertebræ and sometimes the iliac crest.

Insertion.—Outer face of femur below greater trochanter.

Innervation (in Artiodactyla).—Inferior gluteal branch of sciatic.

ECHIDNA (Westling, 1889, pp. 30–31)

Origin.—Spines of sacral and anterior caudal vertebræ.

Insertion.—Tibia and fibula near tarsus.

Innervation.—Branch of tibial nerve (n. glut. inf.).

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.—Spines of posterior sacral and anterior caudal vertebræ and superior iliac crest.

Insertion.—Upper end of femur near great trochanter.

SPHENODON (Osawa, 1898, pp. 569–570) (Pls. XLIII, XLV)

Ilio-tibialis branch of extensor triceps

Origin.—Lateral surface of ilium, above origin of iliofemoralis.

Insertion.—Anterior surface of head of tibia with femoro-tibialis (= part of quadriceps).

Innervation.—Ramus iliotibialis of N. cruralis and ramus ilio-tibialis of N. peroneus communis.

Femoro-coccygeus (Agitator caudæ)

HYPsiprymnodon (Carlson, 1915, p. 20)

Der M. femoro-coccygeus Agitator caudæ, Frets....geht einschichtig von einigen Schwanzwirbeln aus und befestigt sich an dem Trochanter major und dem ersten Drittel des Femur. In Bezug auf die Insertion hat er sich bei *Hypsiprymnodon* proximalwärts gezogen, da er bei *Thylacinus* und *Phalanger*, *Trichosurus* und *Æpyprymnus*, *Petrogale* und *Dendrolagus* das distale Ende des Femur erreicht....

ORNITHORHYNCHUS (Cuvier and Laurillard, Planches de Myologie, Pl. 269, fig. 1; Westling, 1889, p. 30).

Origin.—Fascia over sacrum and coccygeal vertebræ.

Insertion.—Outer side of tibia near distal end.

Remarks.—?Part of gluteus maximus of *Ornithorhynchus*.

CYNOGNATHUS (inferred condition)

Probably not yet differentiated from extensor iliotibialis (Part I).

REPTILES

Posterior part of iliotibialis externus.

Biceps femoris (Caput longum)

UNGULATA (Windle and Parsons, 1903, p. 272)

Origin.—Tuber ischii.

Insertion.—Fascia of upper half or more on outer side of leg, and a fibrous portion to the calcaneal tuberosity.

Innervation.—Cat, man, nerve to the hamstring muscles (a branch of N. ischiadicus).

ECHIDNA (Westling, 1889, p. 36)

Origin.—Tuber ischii.

Insertion.—Fascia on outer surface of tibia from knee to ankle.

Innervation.—N. tibialis.

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.—Tuber ischii.

Insertion.—Fascia over fibula, to tibia.

SPHENODON (Osawa, 1898, pp. 575–576) (Pls. XLIII, XLV)

Iliofibularis

Origin.—Lateral surface of ilium behind origin of iliofemoralis.

Insertion.—Lateral surface of proximal second fourth of fibula.

Innervation.—N. iliofibularis of N. peroneus communis.

Tenuissimus (Caput breve bicipitis, bicipiti accessorius)

CAT (Reighard and Jennings, 1901, p. 195)

Origin.—Tip of transverse process of second caudal vertebra.

Insertion.—With medial surface of biceps.

Innervation.—N. ischiadicus (peroneal branch).

Remarks.—This muscle is usually regarded as the homologue of the short head of the biceps in man and other Primates (Parsons, 1911, p. 59); this has shifted its origin from the caudal vertebræ to the back of the femur, using the agitator caudæ as a muscle slide (Parsons). Keith (1913, p. 440) says that some authors regard it as part of the muscular sheet which forms the peroneal muscles.

CYNOGNATHUS

Occurrence and position problematical.

ALLIGATOR

?Iliofibularis, part II

Origin.—From lateral crest of ilium, behind extensor ilio-tibialis I.

Insertion.—Antero-superior lateral surface of tibia near peroneus anterior.

Innervation.—Branch from N. ischiadicus.

Remarks.—Gadow (1882, p. 385) notes that in many carnivores (cat, dog, hyæna, coati, etc.) as figured in the “Planches de Myologie” of Cuvier and Laurillard, there is a muscle called the “accessoire coccygien du biceps” [bicipiti accessorius, tenuissimus] which corresponds almost completely to the M. iliofibularis of reptiles.

Semitendinosus

PERISSODACTYLA (Windle and Parsons, 1903, pp. 271–272)

Origin.—Tuber ischii and ant. caudal vertebræ.

Insertion.—Second quarter of internal surface of shaft of tibia and a small portion to calcaneal tuberosity as a sheath for the tendo achilleis.

Innervation.—(Man) hamstrings branch from N. tibialis.

ECHIDNA (Westling, 1889, pp. 35-36)

Origin.—Tuber ischii, united with semimembranosus.

Insertion.—Dorsal surface of tibia distal to insertion of semimembranosus.

Innervation.—Nn. obturator and ischiadicus.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—Outer surface of ischium with semimembranosus near tuber ischii.

Insertion.—Lateral surface of proximal end of tibia.

SPHENODON (Osawa, 1898, pp. 563-574) (Pls. XLIII, XLV)

Ischio-tibialis-posticus, lateral portion (Osawa, 1898, pp. 574-575) = flexor tibialis externus (Gadow, 1882, pp. 395-398)

Origin.—Same as medial portion (see below)

Insertion.—Lateral side of proximal end of tibia.

Innervation.—Same as medial portion (see below).

Semimembranosus**PERISSODACTYLA** (Windle and Parsons, 1903, pp. 270-271)

Origin.—Tuber ischii and anterior caudal vertebræ.

Insertion.—Internal lateral ligament.

Innervation.—(Man) hamstrings branch of sciatic.

ECHIDNA (Westling, 1889, pp. 35-36)

Origin.—Tuber ischii.

Insertion.—Head of tibia beneath internal lateral ligament.

Innervation.—Nn. obturatorius and ischiadicus.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—Tuber ischii.

Insertion.—Medial side of head of tibia.

SPHENODON (Osawa, 1898 (Pls. XLIII, XLV)

"Ischio-tibialis-posticus," medial portion (Osawa, 1898, pp. 574-575) = flexor tibialis internus (Gadow, 1882, pp. 398-402)

Origin.—Outer surface of tuber ischii, fascia of tail and tendon of *M. coccygeo-femoralis brevis*.

Insertion.—Medial side of proximal end of tibia and tendon from tibia to lateral condyle.

Innervation.—Nn. ischio-tibiales from plexus sacralis.

C.—Muscles on the Inner Side of the Thigh (Adductors, etc.)**Gracilis**

UNGULATA (Windle and Parsons, 1903, pp. 274–275)

Origin.—Whole length of symphysis.

Insertion.—Upper part of inner surface of tibia with sartorius and by a fascicle as part of a sheath for enclosure of tendo achillis.

Innervation.—N. obturatorius.

ECHIDNA (Westling, 1889, pp. 34–35)

Origin.—Bases of marsupial bones, pubic symphysis and part of hinder border of pelvis.

Insertion.—Dorsal surface of tibia distal to insertions of semi-membranosus and semitendinosus.

Innervation.—By two branches of N. obturatorius.

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.—Whole length of ischio-pubic symphysis and posterior end of marsupial bones.

Insertion.—Median side of tibia near its head.

SPHENODON (Osawa, 1898, p. 537) (Pls. XLIII, XLV)

Pubo-ischio-tibialis

Origin.—Ligamentum pubi-ischiadicum and ischio-pubic symphysis.

Insertions.—Medial side of proximal end of tibia.

Innervation.—R. pubi-ischio-tibialis of N. obturatorius.

Adductor longus

CAT (Reighard and Jennings, 1902, pp. 199–200)

Origin.—Medial three-fourths of cranial border of pubis.

Insertion.—Linea aspera along second and third fifths of femur.

Innervation.—N. obturatorius.

ORNITHORHYNCHUS (Coues, 1868, p. 161) (Pl. XLV)

Origin.—Horizontal ramus of pubis near medial line and on the marsupial bone.

Insertion.—Inner condyle of femur.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—With adductor magnus on median ventral rami of pubis and ischium.

Insertion.—Median surface of shaft of femur.

SPHENODON (Osawa, 1898, pp. 570–571) (Pls. XLIII, XLV)

Pubi-ischio-femoralis.

Origin.—Pubi-ischiadic ligament.

Insertion.—Middle of hinder side of femur.

Innervation.—Ramus ischio-femoralis of N. obturatorius.

Adductor brevis

CAT (part of adductor femoris)

MAN

Origin.—Body of pubis.

Insertion.—Posterior surface of shaft of femur on line leading from lesser trochanter to linea aspera and on upper three-fourths of linea aspera.

Innervation.—N. obturatorius.

ECHIDNA (Westling, 1889, p. 35)

Origin.—Marsupial bone, pubis and ischium dorsal to gracilis and ventral to adductor magnus.

Insertion.—By two heads, one on femur medial to insertion of iliacus and pectineus, the other on the internal condyle. (This muscle may include the adductor longus of Coues.)

Innervation.—N. obturatorius (Westling, 1884, p. 37).

CYNOGNATHUS (inferred condition)

Probably not recognizable as such.

SPHENODON

Part of pubi-ischio-femoralis.

Adductor magnus

UNGULATA

Part of "adductor mass."

CAT (Reighard and Jennings, 1901, pp. 198–199)

Adductor femoris (= magnus + brevis).

Origin.—Rami of pubis and ischium along whole length of symphysis; from ramus of ischium between symphysis and tuberosity and from tendon of origin common to the two gracilis muscles.

Insertion.—Ventral surface of shaft of femur, from greater trochanter to intercondyloid fossa.

Innervation.—Ventral rami of sixth and seventh lumbar nerves (N. obturatorius).

ORNITHORHYNCHUS (Coues, 1870, pp. 160–161) (Pl. XLV)

Origin.—Ischio-pubic ramus in front of origin of semitendinosus.

Insertion.—Posterointernal face of femur along its proximal half.

ECHIDNA (Westling, 1889, p. 35)

Origin.—Posterior border of pelvis and ventral surface of ischium caudal to obturator foramen.

Insertion.—By a small part on dorsal surface of femur and by a larger part on internal condyle and on its crest with adductor brevis.

Innervation.—Obturator and ischiadic nerves.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—Ventral border of ischium above gracilis and anterior to semitendinosus and semimembranosus.

Insertion.—Median face of middle of shaft of femur.

SPHENODON (Pl. XLIII)

Part of pubi-ischio-femoralis.

Obturator externus

CAT (Reighard and Jennings, 1902, p. 191)

Origin.—Outer margin of thyroid fenestra.

Insertion.—By strong tendon into digital fossa of femur.

Innervation.—N. obturatorius.

ECHIDNA (Westling, 1889)

Origin.—Medial parts of the pubis and ischium and anterior border of the pubis.

Insertion.—By a tendon, which unites with that of the obturator intermedius and is inserted on the femur between the two trochanters.

Innervation.—N. obturatorius.

CYNOGNATHUS (inferred condition) (Pl. XLV)

As in reptiles.

ALLIGATOR (Gadow, 1882, pp. 414–415) (Pl. XLVI)

Pubi-ischio-femoralis externus.

SPHENODON (Pls. XLIII, XLV)

Part of pubi-ischio-femoralis (see p. 492).

Quadratus femoris

CAT (Reighard and Jennings, 1901, p. 191)

Origin.—Lateral surface of ischium near tuberosity.

Insertion.—Distal two-thirds of ventral border of great trochanter and about half adjacent border of lesser trochanter.

Innervation.—(Man) Tibial nerve, branch to quadratus femoris; from lumbar and sacral plexuses through upper part of sciatic nerve (Cunningham 1903, pp. 597, 607 and Fig. 439).

ECHIDNA (Westling, 1889, p. 32)

Origin.—Dorsal border of ischium from acetabulum to origin of biceps, semimembranosus and semitendinosus.

Insertion.—Proximo-lateral part of dorsal surface of femur and on lateral crest distal to greater trochanter lateral to Mm. obturatores.

Innervation.—Branch of N. tibialis.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Origin.—Dorsal border of ischium from acetabulum to spine.

Insertion.—Crest of great trochanter distal to same, and inner (medial) surface of lesser trochanter.

SPHENODON (Osawa, 1901, p. 563) (Pls. XLIII, XLV)

Ischio-trochantericus (= pubi-ischio-femoralis posterior, Gadow, 1882, pp. 416–420)

Origin.—Inner surface of tuber ischii, also from caudal border and a small strip on outer surface of same.

Insertion.—“Trochanter minor” (= trochanter externus).

Innervation.—In the Alligator this muscle is innervated chiefly by a short thick branch from stem *a* (= N. tibialis) of the sacral plexus and by a small twig from the obturator nerve. In *Sphenodon* the muscle is innervated from the sacral plexus (Osawa), as it is also in lizards and Chelonia (Gadow).

Gemellus inferior

CAT (Reighard and Jennings, 1902, p. 190)

Origin.—Dorsal half of whole lateral surface of ischium between the ischial spine and the ischial tuberosity.

Insertion.—Inner surface of tendon of the obturator internus.

Innervation.—(Man) Tibial nerve, branch to quadratus femoris and gemellus inferior (Cunningham, p. 607).

CYNOGNATHUS (inferred condition)

Possibly not differentiated from quadratus femoris.

SPHENODON

Probably not differentiated from pubi-ischio-femoralis posterior.

Obturator internus

CAT (Reighard and Jennings, 1901, pp. 192–193)

Origin.—Dorsal surface of ramus of ischium along symphysis and on medial border of ischium from symphysis to tuberosity.

Insertion.—By tendon through lesser sciatic notch into trochanteric fossa with gemellus inferior.

Innervation.—(Man) Obturator internus nerve from sacral plexus (Cunningham, 1903, p. 597)

ECHIDNA (Westling)

Absent.

ORNITHORHYNCHUS (Coues, 1870, p. 162)

(= *quadratus femoris*?)

Origin.—Concave posterior border of ischio-iliac ramus and posterior surface of ectotrochanter.

Insertion.—Border and posterior surface of ectotrochanter.

CYNOGNATHUS (inferred condition) (Pl. XLV)

Part of *quadratus femoris*.

SPHENODON (Pls. XLIII, XLV)

Part of ischio-trochantericus.

D. Deep Gluteal and Tail Muscles

Tensor fasciæ femoris

UNGULATES (Windle and Parsons, 1903, p. 266)

Origin.—It rises from the iliac crest, . . . and spreads out into a fan-shaped muscular mass which usually becomes lost in the fascia lata about the middle of the thigh.

Insertion.—Into the fascia lata on the outer side of the thigh.

Innervation.—From the superior gluteal nerve.

Remarks.—The tensor fasciæ femoris, although at first sight belonging to the superficial layer along with the gluteus maximus, is innervated by the same nerve which supplies the deep gluteal muscles, both in man and ungulates.

ORNITHORHYNCHUS (Westling, 1884; Coues, 1871)

This muscle is not recorded.

CYNOGNATHUS (inferred condition)

Origin.—?Antero-superior margin of ilium.

Insertion.—?Fascia covering the femoro-tibialis.

Remark.—Possibly not yet differentiated from the ilio-femoralis.

SPHENODON

?Not differentiated from ilio-femoralis, which, in turn, represents the anterior part of the caudi-ilio-femoralis (Gadow).

Gluteus medius

CARNIVORA (Windle and Parsons, 1898, pp. 158–159)

Mesogluteus

Origin.—Gluteal surface of ilium and fascia lata.

Insertion.—Greater trochanter on its outer and posterior surface.

Innervation.—Superior gluteal nerve.

Remark.—Closely associated with the pyriformis in the Carnivora.

ECHIDNA (Westling, 1889, pp. 31-32)

Origin.—Spinous processes of last sacral vertebræ.

Insertion.—Distal edge of greater trochanter and posteriorly along femur.

Innervation.—Branch of peroneal nerve.

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.—Posterior part of outer surface of ilium, as part of caudilio-femoralis.

Insertion.—On greater trochanter of femur.

SPHENODON (Osawa, 1898, p. 570) (Pls. XLIII, XLV)

Iliofemoralis

Origin.—Lateral surface of dorsal part of ilium.

Insertion.—Latero-posterior border of proximal part of femur.

Innervation.—R. muscularis brevis from N. femoralis and R. iliofemoralis from N. peroneus.

Gluteus minimus

CARNIVORA (Windle and Parsons, 1898, p. 158)

Entogluteus

Origin.—Ventral part of gluteal surface of ilium.

Insertion.—Front and outer side of greater trochanter.

Innervation.—Superior gluteal nerve.

ECHIDNA (Westling, 1899, pp. 31-32)

“Rest of gluteal group”

Origin.—Lumbodorsal fascia, spinous processes of dorsal vertebræ, first sacral vertebræ and ilium.

Insertion.—Great trochanter.

Innervation.—Crural branch of N. ischiadicus.

CYNOGNATHUS (inferred condition) (Pls. XLIV, XLV)

Origin.—Posterior part of outer surface of ilium, as part of caudilio-femoralis.

Insertion.—Great trochanter.

SPHENODON (Pls. XLIII, XLV)

Part of iliofemoralis.

Gluteus ventralis

CARNIVORA (Windle and Parsons, P. A. S., 1898, p. 158)

Scansorius, capsularis

Gluteus quartus

Origin.—Ventral border of the ilium, close to the origin of the rectus femoris.

Insertion.— Lower part of the front of the great trochanter.

Remarks.— “This is a differentiation of the ventral fibres of the entogluteus” (idem).

REPTILES

Ilio-femoralis (partim)

The gluteus ventralis of mammals looks like a derivative of the ilio-femoralis of reptiles.

Gluteus profundus

CARNIVORA (Windle and Parsons, 1898, p. 159)

Gluteus quintus

Ilio-capsularis

Origin.— From the ilium just above the acetabulum, and passes over the capsule of the hip-joint.

Insertion.— Upper part of the anterior surface of the shaft of the femur between the origins of the vastus internus and crureus.

REPTILES

Remark.— The gluteus profundus of mammals appears to be derived from the deepest part of the ilio-femoralis of reptiles.

Pyramiformis

CAT (Reighard and Jennings, 1901, pp. 188–189)

Origin.— Tips of transverse processes of last two sacral and first caudal vertebræ.

Insertion.— Proximal part of great trochanter caudal to insertion of *gemellus superior*.

Innervation.— (In Man) sacral plexus from first and second sacral nerves, associated with the origin of the peroneal nerve (Cunningham, 1903, p. 607).

HYPSPRYMNODON (Carlsson, 1915, p. 21)

Remark.— “Der Muskel wird wie gewöhnlich durch seine Lage dorsalwärts vom Stamm des N. ischiadicus und seine Vereinigung mit dem M. gluteus medius charakterisiert.”

ECHIDNA (Westling, 1888, p. 32)

Absent.

ORNITHORHYNCHUS (Coues, 1870, p. 160)

(= “*Quadratus femoris*”)

Origin.— Transverse processes of coccygeal vertebræ.

Insertion.— Middle of back of femur.

CYNOGNATHUS (inferred condition)

Part of "*caudi-ilio-femoralis*."

SPHENODON (Osawa, 1898, pp. 569-570) (Pls. XLIII, XLV)

Part of "*Coccygeo-femoralis brevis*" (= *caudi-ilio-femoralis*, Gadow).

Origin.—Ventral surfaces of transverse processes of six anterior tail vertebrae.

Insertion.—Tendon of *M. ischio-tibialis-posticus*.

Innervation.—Branch of *N. pudendus externus*, and from *N. postsacralis*.

Remarks.—The pyriformis of mammals appears to represent part of the *caudi-ilio-femoralis* of reptiles. In Crocodilia and lizards the *caudi-ilio-femoralis* is innervated chiefly by the first presacral stem (α) which is associated with the origin of the tibial and peroneal nerves; in mammals the nerve that supplies the pyriformis has similar relations.

Gemellus superior

CAT (Reighard and Jennings, 1901, pp. 189, 401)

Origin.—Elongate area on dorsal border of ilium and ischium between posterior inferior iliac spine and spine of ischium.

Insertion.—Triangular area dorsal to tip of great trochanter.

Innervation.—*N. tibialis*.

Remarks.—The position and innervation of this muscle indicate that it has been derived from the *pubi-ischio-femoralis posterior* of reptiles, along with the *obturator internus*.

CYNOGNATHUS (inferred condition)

Not differentiated from *pubi-ischio-femoralis posterior*.

SPHENODON

Probably not differentiated from *pubi-ischio-femoralis posterior* (*ischio-trochantericus*). See p. 494.

Caudi-femoralis ("M. ischio-femoralis Parsons" Carlsson)

CAT (Reighard and Jennings, 1902, p. 195)

Origin.—"By a flat tendon from the transverse processes of the second and third caudal vertebrae. The muscle forms a flat band which passes distad over the pelvis and caudad of the great trochanter. At the middle of the thigh it ends in a very thin tendon. The tendon passes distad along the medial surface of the biceps femoris, pierces the fascia lata near the knee, and passes to its

Insertion.—Into the middle of the lateral border of the patella" (Reighard and Jennings).

HYPsiprymnodon (Carlsson, 1915, p. 20)

"Entspringt, von dem vorgehenden Muskel [Femoro-coccygeus, Agitator caudæ] bedeckt, tritt schwanzwärts von ihm ein wenig zutage; er wird von dem N. ischiadicus-Stamme überlagert. Er inserirt mehr distalwärts als der M. femoro-coccygeus, indem er sich längs der ersten Hälfte des Femur anheft.... durch seine Lage in Verhältnis zum N. ischiadicus dokumentiert er sich als ein M. caudo-femoralis."

ECHIDNA (Westling, 1889, p. 33)

Origin.—Spinous process of first caudal; lies ventrad to the two forks of the ischiadic nerve.

Insertion.—Dorsal surface of femur on a prominence near the crest of the trochanter major, distal to the quadratus femurus and to the obturators, proximal to the gluteus medius.

Innervation.—N. tibialis.

CYNOGNATHUS (inferred condition) (Pl. XLIV)

About as in *Sphenodon*.

SPHENODON (Osawa, 1898, pp. 569–570) (Pl. XLIII)

"*Coccygeo-femoralis longus*" (= caudi-femoralis, Gadow)

Origin.—Transverse processes and ventral surfaces of anterior caudal vertebræ.

Insertion.—On and near great trochanter and by a small strand upon capsule of knee, and lateral side of epicondylus ulnaris femoris.

Innervation.—Rr. musculares of N. postsacralis.

Extensor caudæ medialis (T, Fig. 8)**CAT** (Reighard and Jennings, 1902, p. 137)

Levator caudæ internus

Origin.—"By numerous fleshy bundles from the spinous processes of the sacral and first caudal vertebræ."

Insertion.—The fibres pass caudad and are inserted by tendons into the articular processes and the dorsal surface of the caudal vertebræ.

Innervation.—Rr. dorsales of Nn. spinalis caudæ (R. & J., p. 404).

Remarks.—"This is a continuation caudad of the multifidus spinæ; it lies next to the dorsal median line, the muscles of right and left side touching one another in the middle line" (Reighard and Jennings).

VARIOUS MAMMALS. Cuvier and Laurillard (Planches de Myologie)

T.¹ Interépineux supérieurs.

REPTILES (Gadow)

Musculus caudæ dorsalis (partim).

¹ Symbol used by Cuvier and Laurillard. See Fig. 8.

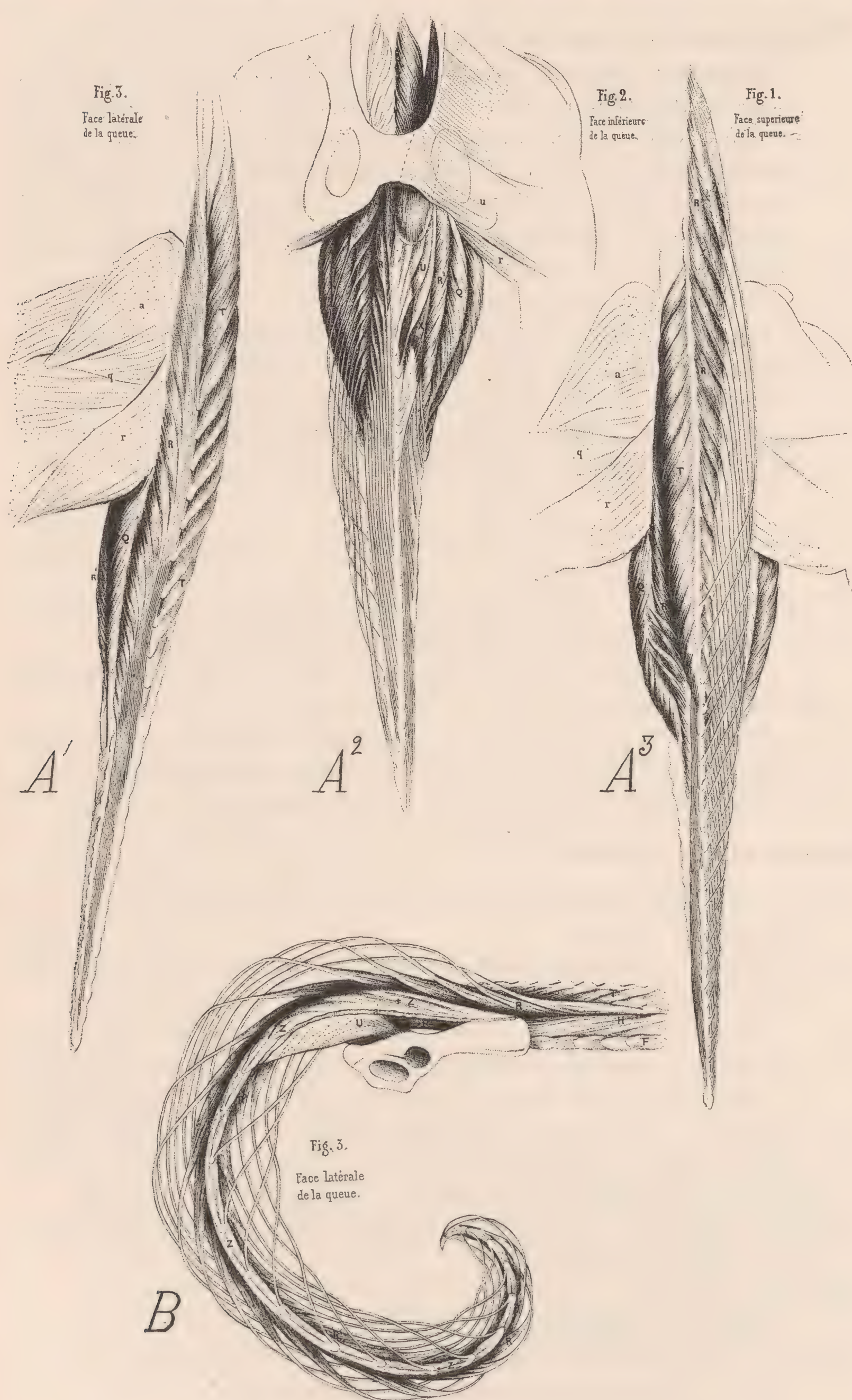


Fig. 8.

Extensor caudæ lateralis (R, Fig. 8)

CAT (Reighard and Jennings, 1902, p. 137)

Levator caudæ externus

Origin.—“In many fleshy bundles from the articular processes of the sacral vertebræ, and the transverse processes of the sacral vertebræ, and the transverse processes of the caudal vertebræ.”

Insertion.—“The fibres curve dorsocaudad and are inserted by many long slender tendons on the dorsal surfaces of the caudal vertebræ. The muscle grows continually smaller as it passes caudad” (Idem).

Innervation.—Rr. dorsales of Nn. spinales caudæ (idem, p. 404).

Remarks.—“This is a continuation caudad of the medial portion of the longissimus dorsi; it lies just laterad of the extensor caudæ medialis.” (Idem, p. 137).

VARIOUS MAMMALS

Sacro-coccygeus superior (R). Cuvier and Laurillard (*Anat. Comp. Planches de Myologie*)

REPTILES

Part of M. caudæ dorsalis (Gadow)

Abductor caudæ externus [superior, dorsalis] (Z, Fig. 8)

CAT (Reighard and Jennings, 1902, p. 137)

Intertransversarii caudæ

Origin.—Medial side of dorsal border of ilium and dorsal surface of sacrum.

Insertion.—Transverse processes and lateral surfaces of caudal vertebræ as far back as eighth or ninth.

Innervation.—R. dorsales of N. coccygeus.

ORNITHORHYNCHUS (Coues, 1870, pp. 134–135)

“*Extensor lateralis*” of the tail

Origin.—Posterior edge of ilium.

Insertion.—Tips of transverse processes of caudal vertebræ.

Fig. 8. Tail muscles of mammals. After Cuvier and Laurillard.

A¹ *Castor*, lateral view, left side.

A² The same, ventral view.

A³ The same, dorsal view.

B *Cebus*, lateral view, right side.

Abbreviations (R, etc.) and names of muscles given on page 506.

CYNOGNATHUS (inferred condition) (Pl. XLIV)

Ilio-caudalis

Origin.— Medial side of posterior process of ilium.

Insertion.— Transverse processes of caudal vertebræ.

SPHENODON (Osawa, 1898, pp. 567, 569) (Pl. XLIII)

"Coccygeo-iliacus" (ilio-caudalis, Gadow)

Origin.— Caudal border and inner surface of dorsal end of ilium.

Insertion.— [Transverse processes of caudal vertebræ.]

Innervation.— Rr. dorsales of N. coccygeus.

Ischio-coccygeus (Q, Fig. 8)

CAT (Reighard and Jennings, 1902, p. 137)

Abductor caudæ [inferior]*"Abductor caudæ internus"* (M. coccygeus)

Origin.— Spine of ischium.

Insertion.— Ventral surfaces of transverse processes of second to fourth caudal vertebræ.

ORNITHORHYNCHUS (Coues, 1870, p. 135)

"Flexor lateralis of the tail"

Origin.— Tuber ischii.

Insertion.— Transverse processes of three [anterior?] caudal vertebræ.

CYNOGNATHUS (inferred conditions) (Pl. XLIV)

Ischio-caudalis

Origin.— Spine of ischium.

Insertion.— Ventral side of transverse processes of anterior caudal vertebræ (?).

SPHENODON (Osawa, 1898, pp. 567, 569) (Pl. XLIII)

Coccygeus-ischiadicus (Pars ischio-caudalis des M. ilio-ischio-caudalis Gadow)

Origin.— Tuber ischii.

Insertion.— Ventral sides of transverse processes of caudal vertebræ.

Innervation.— N. coccygeo-ischiadicus, from N. postsacralis II.

Remarks.— The ilio-ischio-caudalis of crocodiles, lizards and *Sphenodon* is a lateral and ventral mass, below the dorsal tail muscles (levators) running from the posterior tip of the ilium and of the ischium. It lies outside of the caudi-femoralis and caudi-ilio-femoralis. The ilio-caudalis, which is still metameric in the alligator, may have given rise to the abductor caudæ externus, or intertransversarii (Z) of mammals; the ischio-caudalis may have given rise to the ischio-coccygeus (Q), ilio-

coccygeus (U) and pubi-coccygeus (X). The caudal part of the caudifemoralis, arising around the chevrons may represent the sacro-coccygeus inferior (R¹) plus interspinalis inferior (V). (See p. 506 and Fig. 8).

Levator ani

MAN (Cunningham, 1903, p. 411)

Origin.—Back of the body of the pubis, pelvic fascia and spine of ischium.

Insertion.—(1) Into central point of the perineum, (2) the external sphincter ani, (3) sides of the lower sacral and coccygeal vertebræ.

The levator ani is divisible into four parts — pubo-rectalis, pubo-coccygeus, ilio-coccygeus and ilio-sacralis.

Innervation.—Perineal (muscular) branches of pubic nerve, and, on its pelvic surface, by special branches from the third and fourth sacral nerves.

CAT (Reighard and Jennings, 1902, pp. 137–138)

“*Ilio-caudalis*,” *levator ani*

Origin.—“Along the ventral half of the medial surface of the ilium, caudad of the sacrum.”

Insertion.—“By a flat tendon into the ventral surface of the caudal vertebræ, from the second or third to about the seventh.”

HYPSPRYMNODON (Carlsson, 1915, p. 27)

Remark.—“Der M. pubo-coccygeus und der M. ileo-coccygeus sind dicht an einander gelagert und enden im vorderen Teil des Schwanzes.”

VARIOUS MAMMALS (Cuvier and Laurillard, *Planches de Myologie*)

U¹ Iléo-sous-caudien (iléo-coxygien).

X¹ Pùbo-sous-caudien (pubo-coxygien).

REPTILES

Aftermuskeln (Gadow, 1882, p. 365)

A group of muscles in the cloacal region derived from the lateral muscle of the tail (ischio-caudalis).

Sacro-coccygeus inferior (R¹) (Fig. 8, A², A¹)

Cuvier and Laurillard (*Planches de Myologie*)

Flexor caudæ longus Reighard and Jennings

Flexor caudæ externus Parsons

UNGULATES (Windle and Parsons, 1903, p. 266)

Origin.—Posterior sacral and anterior caudal spines. (Part of the great muscular sheet which lies between the ectogluteus and the true biceps).

¹ Symbols used by Cuvier and Laurillard. Cf. Fig. 8 and p. 506.

Provisional Homologies of the Pelvic Muscles in Reptiles, Birds, and Mammals

Innervation from	SPHENODON (Osawa. Gadow)	ALLIGATOR (Gadow)	OSTRICH (Gadow)	MONOTREME (Westling)	PLACENTAL (Cunningham)
<i>Plexus cruralis</i> (<i>N. femoralis</i>)	Pubi-ischio-trochantericus-int. (Osawa)	Pubi-ischio-femoralis int.	Ilio-femoralis-internus (Gadow)	{ Pectineus Iliacus Psoas major	Pectineus Iliacus Psoas major
	Extensor triceps Ambiens	Ilio-tibialis internus { Femoro-tib. Ambiens (2 parts)	Ilio-trochantericus partim Sartorius Femoro-tib. Ambiens (2 parts)	Sartorius Quadriceps Rectus fem.	Sartorius Quadriceps Rectus fem.
<i>Nn. a + b</i>	Ilio-tibialis	Ilio-tibialis I	Ilio-tibialis externus	Gl. max.	{ Glut. max. Agitator caud.
	Coccyg. fem. brev.	Caudi-ilio-fem.	Caudi-ilio-fem.	?	<i>N. peroneus</i> Pyriformis
<i>Nervus obturatorius</i>	Pubi-ischio-tibialis	Absent	Absent	Gracilis	Gracilis
	Pubi-ischio-femoralis (Osawa)	{ Ischio-femoralis (Gadow)	Absent	{ Add. long. Add. brevis Add. mag.	Adductor longus Adductor brevis Adductor magnus
		Pub. ischio-femoralis externus (Gadow)	Pub. ischio-femoralis Add. mag. avium ¹ Obturator + Accessorii	Absent	Absent
				<i>N. obt.</i> Obt. externus	<i>N. obt.</i> Obturator ext.

¹ The "adductor magnus" of birds (= pubi-ischio-femoralis, Gadow) does not appear to be homologous with any of the adductor series of mammals, since it arises above and behind the pubi-ischio-femoralis externus (= obturator externus) instead of below and in front of it as in mammals [W. K. G.].

<i>Plexus ischiadicus</i>					
Innervation from	SPHENODON (Osawa, Gadow)	ALLIGATOR (Gadow)	OSTRICH (Gadow)	MONOTREME (Westling)	PLACENTAL (Cunningham)
<i>N. iliofem. + N. fem.</i>	Ischio-trochantericus (Osawa)	Pub. isch. fem. post. (Gadow)	Ischio-femoralis ²	Quad. femoris <i>N. tibialis</i>	Quadr. femoris Gemellus inf. Obturator int. Gemellus sup. <i>N. tibialis</i>
	Ilio-femoralis	<i>Plx. isc. + cr.</i> Ilio-femoralis [part]	Ilio. fem. ext. + Ilio-trochantericus [part]	Gluteus minimus <i>N. glut. sup.</i>	Gluteus minimus Gluteus medius Tensor fasc. fem. <i>N. glut. super.</i>
	Ilio-fibularis	Ilio-fibularis (I) Ilio-fibularis (II)	Ilio-fibularis	<i>N. to hamstring muscles</i> Biceps	Tenuissimus (Bic. cap. brev.) Biceps femoris (cap. long.) <i>N. to bic. access.</i>
	Ischio-tib. posticus { lateral { medial	Flex. tib. ext. Flex. tib. int.	Caud. ilio-flexorius Ischio-flex.	<i>N. to hamstring muscles</i> Semitend. Semimemb.	Semitendinosus Simemembranosus <i>N. to hamstring muscles</i>

² The “ischio-femoralis” of birds appears to be homologous rather with the pubi-ischio-femoralis posterior of reptiles than with the ischio-femoralis of reptiles [W. K. G.].

Insertion.— Chiefly into the outer side of the patella; above and below this it blends with the fascia.

Innervation.— It is supplied by the same nerve as the ectogluteus (inferior gluteal).

CAT (Reighard and Jennings, 1902, p. 138)

Origin.— “Ventral surface of the last lumbar vertebræ, of the sacrum, and of the transverse processes of the caudal vertebræ. Caudad the muscle forms long, strong tendons. . . .”

Insertion.— On ventral surface of the caudal vertebræ.

ORNITHORHYNCHUS (Cuvier and Laurillard, Planches de Myologie, Ornithorhynque, Pl. 269, figs. 1, 2, R¹)

Provisional Homologies of

MAN (H. H. Wilder)	VARIOUS MAMMALS (Cuvier and Laurillard)	CAT (Reighard and Jennings)	PETROGALE (Parsons)
Sacro-coccygei posteriores (ex- tensor coccygis)	(T) Interépineux supérieur	Extensor caudæ medalis	Extensor caudæ internus
	(R) Sacro-coxygien supérieur	Extensor caudæ lateralis	Extensor caudæ externus
Abductor caudæ dorsalis	(Z) Intertransversaires	Abductor caudæ externus	Abductor caudæ internus
Abductor caudæ ventralis (coc- cygeus)	(Q) Ischio-caudien (ischio- coxygien externe)	Abductor caudæ internus	Abductor caudæ externus
Sacro-coccygei anteriores	(R') Sacro-coxygien inférieur	Flexor caudæ longus	?Flexor caudæ externus
	(V) Sous-caudien (interépi- neux inf.)	{ ?Flexor caudæ brevis [?Flexor caudæ profundus	{ Flexor caudæ internus ?Flexor caudæ profundus
Levator ani group	(U) Iléo-sous-caudien (iléo- coxygien)	Ilio-caudalis	
(in part)	(X) Pubo-sous-caudien (pubo- coxygien)	Levator ani	

“*Depressor caudæ*” (Coues, 1870, p. 135) .

Origin.— Inside of pelvis behind acetabulum and at junction of ilium with sacrum.

Insertion.— Apices and ventral surfaces of transverse processes of all caudal vertebræ.

REPTILES

?Part of *caudi-femoralis*

Remark.— The position of this muscle in mammals seems to point to its derivation from the caudi-femoralis. It is also immediately behind and below the pyriformis which was derived from the caudi-ilio-femoralis.

the Chief Tail Muscles

HYPSIPRYMNODON (Carlsson)	ALLIGATOR (Gadow)	SPHENODON (Osawa)
Levator caudæ internus	} M. caudæ dorsalis	} Coccygeo-iliacus
Levator caudæ externus		
Intertransversarii		
	Ilio-caudalis	
Ischio-coccygeus	Ischio-caudalis	Coccygeo-ischiadicus
Sacro-coccygeus (“ Flexor caudæ externus Par- sons”)	} ?Part of caudi-femoralis	?Part of coccygeo-femoralis longus
Flexor caudæ profundus		
Interaccessorii		
Ilio-coccygeus	} “Aftermuskeln” (from ischio-caudalis)	Coccygeo-ischiadicus (partim)
Pubo-coccygeus		

DISCUSSION

By W. K. Gregory

A discussion of the musculature of the shoulder-girdle of *Cynognathus* may be facilitated by reviewing the chief characters in the shoulder-girdle and humerus which contrast *Sphenodon*, a primitive crawling reptile, with man, a highly specialized bipedal mammal.

Sphenodon

Scapula vertical.
 Scapulocoracoid fastened to sternum.
 Clavicle immovably fastened to sternum and to scapula.
 Interclavicle present.
 Coracoid of large size, pierced by the supracoracoid foramen.
 Epicoracoid continuous to clavicle, shutting off the space medial to the scapulocoracoid from the outside.
 Anterior border of scapula in its primitive position.
 No prespinous (supraspinatus) fossa.
 Glenoid facing outward and backward, borne equally by scapula and coracoid.

Homo

Scapula recumbent over ribs.
 Scapulocoracoid free from sternum.
 Clavicle movably fastened to sternum and to acromial process.
 Interclavicle absent.
 Coracoid small or vestigial, not pierced by foramen.
 Epicoracoid absent or perhaps represented by the sternoclavicular ligament; a wide communication between the space medial to the scapulocoracoid and the outside.
 Anterior border of scapula reflected externally, forming the spina scapulæ.
 Prespinous (supraspinatus) fossa widely developed.
 Glenoid facing chiefly downward and forward, borne chiefly by scapula.

The chief contrasts between the humeri of *Sphenodon* and man are as follows:— first, in man, the great extension, subspherical development, and inward growth of the head of the humerus, which now faces more inward and backward; second, the appearance of a distinct “greater tuberosity” for the insertion of the supra- and infraspinatus muscles at the upper end of the deltoid crest, or processus lateralis; third, the extension of the deltoid crest down the shaft and the subsidence of it except at the lower end where it widens out; fourth, the approximation of the greater tuberosity toward the lesser tuberosity (processus medialis) and the formation of a bicipital gutter; fifth, the enclosure of the tendon of the long head of the biceps of man within the capsule of the shoulder-girdle; sixth, the further differentiation of the distal facets of the humerus (which is correlated with the freer power of pronation and supination) and their position more on the end than on the side of the shaft (which is connected with the upright pose).

These osteological differences between *Sphenodon* and man are associated with equal differences in the musculature. In *Sphenodon* the scapula and suprascapula have a relatively great area for the insertion of muscles connecting the shoulder-girdle with the body (including the trapezius, or cucullaris, the levators, the omotrachelian, the serrati, and the subscapularis), while the area for the scapulo-humeral muscles is relatively restricted. The areas for the coracohumeral muscles, both ventral and dorsal to the coracoids, are extensive. In man, on the other hand, the areas on the scapula for the body muscles are restricted chiefly to the margins of the scapula and to the subscapular surface, while the scapulohumeral muscles are greatly enlarged and occupy not only the medial and lateral surface behind the spine but also a great new area, the supraspinatus fossa in front of the spine, which is not at all developed in *Sphenodon*.

These osteological and myological differences between *Sphenodon* and *Homo* are naturally correlated with equal contrasts in the pose: *Sphenodon* retains the primitive reptilian pose of the fore limbs, in which the elbows are widely everted, the arms being held akimbo; while man has gone even beyond the normal mammalian position in which the elbows are drawn in to the flanks, and, in consequence of his upright position, has also opened up the angle between the humerus and the fore limb.

The wide contrast between the primitive reptile *Sphenodon* and the highly specialized placental mammal, *Homo*, in the form of all the elements, in the arrangement of the muscles, and in the pose of the fore limbs, is mediated by the conditions in the living monotremes. These, indeed, more nearly resemble *Sphenodon* than *Homo* in the general form of the shoulder-girdle. Their scapulocoracoid is well fastened to the sternum and is not reflected over the ribs (except in its posterosuperior angle) but is even inclined forward; the clavicle is immovably fastened at both ends; an interclavicle is present; the glenoid is shared equally by the scapula and coracoid and faces more outward than downward; the epicoracoid is largely developed. The prespinous fossa is not yet developed and the supraspinatus muscle is still near its primitive position, associated with the coracoid muscles. In the arrangement of other muscles, also, the monotremes, in many respects, stand in the reptilian stage. The muscles connecting the scapula with the body are very strongly developed, especially the omotrachelian and so-called levators of the scapulæ, almost as well as in reptiles.

On the other hand, the monotreme shoulder-girdle shows an important advance toward the human type in the reflection of the anterior border to form the spina scapulæ (Wilson and McKay), in the development of a large fenestra between the epicoracoid, acromion, and the clavicle, in the reduction of the anteroposterior diameter of the coracoid, and in the loss of

the supracoracoid foramen. The muscles connecting the scapula with the humerus become greatly developed, especially the infraspinatus and the subscapularis. Some presumably aberrant specialization also takes place, especially in the extension of the subscapular area on to the posterosuperior and posteroexternal region of the scapula.

The humerus of monotremes loses but little of the primitive reptilian habitus, the chief advances in the mammalian direction being the further differentiation of the head, the inclination of the head to the long axis of the bone, the development of a distinct greater tuberosity, and the sharp twisting of the shaft.

The pose of the fore limbs of monotremes is essentially reptilian, although the articulations between the scapulocoracoid and the humerus and between the humerus and the forearm are more completely differentiated.

With this comparison of *Sphenodon*, *Homo*, and the monotremes in mind, we are in a position to evaluate the characters of the shoulder-girdle and humerus of *Cynognathus* (Pls. XLI, XLII). In these parts the reptile *Cynognathus* is naturally much closer both to *Sphenodon* and to the monotremes than to *Homo*, since the scapulocoracoids were fastened to the sternum and a wide interclavicle and stout clavicles were present (Broom). In the shoulder-girdle *Cynognathus* is almost intermediate between *Sphenodon* and monotremes. Thus, it shares with *Sphenodon* the primitive reptilian character of the upper end of the scapula, while it resembles monotremes in the sharp reflection of the anterior border to form the spina scapulæ, which ends below in the acromial process for the clavicle. The coracoid region is on the whole nearer to the monotreme type in general form, but very probably differed in the lack or feeble development of an epicoracoid fenestra. Both the pro- and the metacoracoids of the primitive Permian reptiles are retained, but the coracoid mass as a whole is functionally analogous with that of monotremes and the general position of the coracoscapular arch could not have been very dissimilar to the monotreme type, to which it presents a general resemblance in all views. The posterior border of the scapula differs from both the monotreme and the *Sphenodon* type in being sharply reflected and flattened posteriorly.

The humerus of *Cynognathus* and of its relative, *Gomphognathus*, differs from the monotreme type in the sessile position and flattened form of the head, which was located entirely on the top of the shaft as in primitive reptiles and was less sharply inclined inward. The greater tuberosity has not yet been differentiated from the deltopectoral crest (processus lateralis) and the lesser tuberosity (processus medialis) is somewhat less developed than in the monotremes; the same is true of the entocondylar expansion at the distal end. The shaft of the humerus is not so sharply twisted and bent

upon itself as in the monotreme type. Therefore, in all these features the humerus of *Cynognathus* was more primitive and somewhat more reptilian than that of monotremes.

Accordingly, the shoulder-girdle and humerus of *Cynognathus* approach the monotreme type in certain respects and in others are prevailingly reptilian. This fact enables us to infer with some approach to accuracy the general character and arrangement of the musculature. The scapulocoracoid of *Cynognathus* was extremely small as compared with the size of the skull so that the heavy muscles running along the side of the neck from the scapula to the occipital region and along the flanks from the back of the scapula to the ribs were of necessity relatively large in proportion to the size of the scapula; that is to say, the omotrachelian and levators must have filled the whole of the anterior surface of the spina scapulæ¹ for the support of the heavy head, while the opposing muscle, the serratus superficialis, must have been powerfully developed, as is indicated by the flattening and eversion of the posterior border.

It was at first a question whether the postspinous fossa was fully occupied by the infraspinatus muscle (= scapulo-humeralis), as it is in mammals, or whether this fossa was partly filled by the dorsalis scapulæ (deltoides scapularis), as it is in the alligator. In favor of the former view is the rather marked resemblance of this region to the monotreme type and the fact that when the humerus is articulated with the scapulocoracoid the postspinous fossa is in the proper position to support a powerful muscle running down to the posterosuperior surface of the great deltoid crest. Similarly, it was a question whether the medial surface of the scapula was largely taken up by the deep serratus anterior muscles or whether the subscapularis had already extended dorsally, limiting the serratus to the upper end of the scapula. In favor of the latter view is the vigorous development of the internal, or lesser, tuberosity (processus medialis) of the humerus where the subscapularis muscle was inserted. A long rugosity on the posterior border of the scapula just above the glenoid is interpreted as the area of origin for the scapular head of the triceps, while the smaller rugosity immediately below this may well mark the place of origin of the teres minor. The origin of the supraspinatus muscle is placed in our restoration below the acromial region, because the wall of bone at this point would prevent the supraspinatus from finding its way through the epicoracoid fenestra and up onto the anterior surface of the spina scapulæ.² Even in *Ornithorhynchus*, where there is a

¹ This is also the conclusion of D. M. S. Watson (*Journal of Anatomy*, Oct. 1917) whose paper was received some time after the present manuscript was completed.

² Watson (*op. cit.*) comes to the same conclusion.

large epicoracoid fenestra, the supraspinatus has not yet driven out the omotrachelian and levators from the anterior surface of the spine.

At the upper end of the scapula a roughened border indicates the attachment of a stout suprascapula which probably gave insertion to the serratus anterior, to part of the trapezius and perhaps at its anterior corner to the rhomboideus. The sharply reflected spine must have given attachment on its outer border to the stout trapezius and to the spinous portion of the deltoid. Its anterior surface doubtless gave attachment for the omotrachelian and levators, while its posterior surface probably bounded the massive infraspinatus.

The muscles of the coracoid region must have been similar to those of monotremes, first, because of the general similarity of the osseous elements of this region and, secondly, because there is a fundamental agreement in the musculature of the coracoid region even between *Sphenodon* and monotremes.

Possibly the most conjectural features of the restoration of the pectoral region are the position and differentiation of the rhomboideus, which is developed only in the crocodilians among recent reptiles but is well developed in monotremes. We represent it as being associated with the levator scapulæ profundus, from which it may have been derived.

Passing to a consideration of our restoration of the pelvic musculature we may again approach the subject by a comparison of the two extremes, *Sphenodon* and *Homo*, as follows:

<i>Sphenodon</i>	<i>Homo</i>
Ilium rod-like, inclined somewhat backward behind acetabulum, with very small gluteal area and large posterior border for attachment of large tail muscles.	Ilium widely expanded transversely, produced in front of acetabulum, with much enlarged gluteal and iliacus areas. Area for vestigial tail muscles very small.
Pubis and ischium relatively large.	Pubis relatively small.
Pubis much produced in front of acetabulum.	Pubis but little produced in front of acetabulum.
Acetabulum relatively large, subtriangular in outline.	Acetabulum small and subcircular, closely surrounding head of femur.
Femur with oval head on top of shaft.	Femur with spherical head, sharply inclined inward and separated from the shaft by a distinct neck.
Femur with no distinct external trochanter.	Great trochanter of large size located at the top of the shaft.
Internal trochanter facing downward and inward.	Lesser or internal trochanter facing upward and inward.

These broad contrasts are naturally associated with differences in the normal pose of the hind limb, the sprawling pose of the primitive reptile contrasting widely with the erect walking and standing pose of man. In this connection it may be noted that, with the possible exception of some tortoises, reptiles apparently do not stand still for any great length of time; they either move forward or settle down to rest. Consequently, modern reptiles show no special adaptation for maintaining the standing pose, so far as the writer has observed.

Perhaps the most important differences in the musculature of the two forms are as follows: in *Homo* the gluteal area is greatly expanded and the insertions of the primitive tail muscles are greatly reduced or absent. The iliacus area on the front inner side of the ilium is also widely expanded. A group of muscles including the psoas major, iliacus, and pectineus muscles has very probably been derived from the pubi-ischio-femoralis internus mass, the principal change being the loss of the posterior portion of the mass extending over the inner surface of the ischium. The general functions and distal attachments of these supposedly homologous groups in reptiles and mammals are similar and they are innervated from similar or homologous nerves and plexuses. (See page 504).

As in the structure of the fore limb, the monotremes again mediate the differences between *Sphenodon* and *Homo*, although they favor the latter in certain important characters, especially in the position and musculature of the ilium.

Cynognathus, in turn, divides the difference between *Sphenodon* and the monotremes; and a comparison of its pelvis (Pl. XLVI) and femur with those of *Sphenodon*, alligator, and ostrich, yields evidence as to the placing of the principal muscle groups. In the form and relations of the ilium *Cynognathus* approaches the alligator in some respects, the monotremes and the ostrich in others. It agrees with the alligator in the backward prolongation of the ilium behind the acetabulum, with the monotremes in the forward growth of the ilium in front of the acetabulum. The posterior tip of the ilium probably gave insertion to the ilio-caudalis (= abductor caudæ dorsalis) muscles, as in reptiles generally, while the greatly expanded blade of the ilium denotes a corresponding expansion of the ilio-femoralis, which is homologous with the deep glutei of mammals. The great enlargement of the external trochanter on which this muscle was inserted also supports this interpretation. On the superior border of the ilium the gluteus maximus probably arose, comparable with the ilio-tibialis externus of alligator and ostrich. (In monotremes the gluteus maximus does not touch the ilium, as it lies entirely above the pelvis.) The ilio-tibialis internus (= sartorius) probably arose near the anterior margin of the blade of the ilium in front of the gluteal area.

The medial anterior surface of the blade of the ilium probably gave origin to the upper part of the pubi-ischio-femoralis internus. The quadratus lumborum, along with the pubi-ischio-femoralis internus, may possibly have extended down to the femur as in the alligator.

The ilium, on the whole, was decidedly more advanced toward the monotreme type than is that of *Sphenodon*.

In the construction of the pubi-ischadic plate *Cynognathus* is much closer to the monotremes than to either *Sphenodon* or alligator, differing from that of monotremes chiefly in the smaller size of the obturator fenestra. The pubis is located almost directly beneath the acetabulum and is not widely produced in front of it as in *Sphenodon*. The ischium and pubis in other characters also suggest those of *Echidna*.

The acetabulum is very large and, as in primitive reptilian types, it extends superiorly on to the under surface of a prominent overhanging process of the ilium, a condition foreshadowing the monotreme type.

The femur (Pl. XLVIII) differs from those of typical reptiles in having a much enlarged great trochanter, indicating a corresponding development of the deep glutei; the medial or lesser trochanter is a low process at the upper end of a long low ridge on the medial surface of the femur in its upper half of the shaft. The ridge perhaps represents the adductor crest, or linea aspera; the process probably gave insertion to the pubi-ischio-femoralis internus. Accordingly, it seems probable that the femur could be turned fairly well forward and the knees more or less straightened out in running and, further, it seems likely that the pubi-ischio-femoralis internus had already begun to differentiate into the pectineus, iliacus, and psoas major, as in monotremes and other mammals.

On account of the general similarity of the pubi-ischadic region (Pl. XLV) to that of *Ornithorhynchus*, the arrangement of the gracilis, adductors and obturator externus on the pelvis must have been substantially the same as in the monotreme type. The posterior process of the ischium probably gave insertion to the biceps femoris, as well as to the ischio-caudalis, semitendinosus, and semimembranosus, as in monotremes, while the dorsal rim of the ischium was very likely covered by the ischio-trochantericus, or pubi-ischio-femoralis posterior, representing the obturator internus + quadratus femoralis + gemelli of mammals, since there is no very essential difference in this region even between types so widely separated as alligator and *Echidna*.

PART II.—A COMPARISON OF THE MUSCLE AREAS OF THE PELVIS OF
ALLIGATOR, STRUTHIO AND ORNITHOLESTES

BY W. K. GREGORY AND C. L. CAMP

The completion of the manuscript of this part was interrupted when the junior author volunteered and was accepted for military duty. It is, however, deemed advisable to publish the accompanying diagrams at the present time and along with the preceding article, with which their subject matter is closely connected.

It will be seen (Pl. XLVI) that, in spite of the general resemblance of the ilium of theropodous dinosaurs to that of birds, their pelvis as a whole is of reptilian type, resembling the birds in the forward extension of the ilium, but differing from them especially in the fact that the pubis has not been turned backward parallel to the ischium. From this it is fair to infer that the pubi-ischio-femoralis internus, the pubi-ischio-femoralis externus, and adjacent muscles were still in their primitive reptilian position. The supposed homologies of the pelvic muscles in reptiles and birds are given in the table on pages 504, 505.

PART III.—NOTE ON THE ORIGIN AND EVOLUTION OF CERTAIN
LOCOMOTOR ADAPTATIONS IN THE PECTORAL AND PELVIC
GIRDLES OF REPTILES AND MAMMALS

BY W. K. GREGORY

The adaptations for forward locomotion in the girdles and limbs of *Cynognathus* have become clearer to the writer after a fairly comprehensive review of the evolution of the locomotor apparatus in the ascending classes of vertebrates.

The earliest or piscine stage¹ in this evolution, as well as the general principles of quadrupedal locomotion and the mechanism of the limbs in mammals have been discussed in earlier papers, from one² of which may be cited the following paragraphs.

¹ Gregory, W. K. 1915. Present status of the problem of the origin of the Tetrapoda. *Ann. N. Y. Acad. Sci.*, XXVI, pp. 338–369, 375–376.

² Gregory, W. K. 1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Ann. N. Y. Acad. Sci.*, XXII, p. 270.

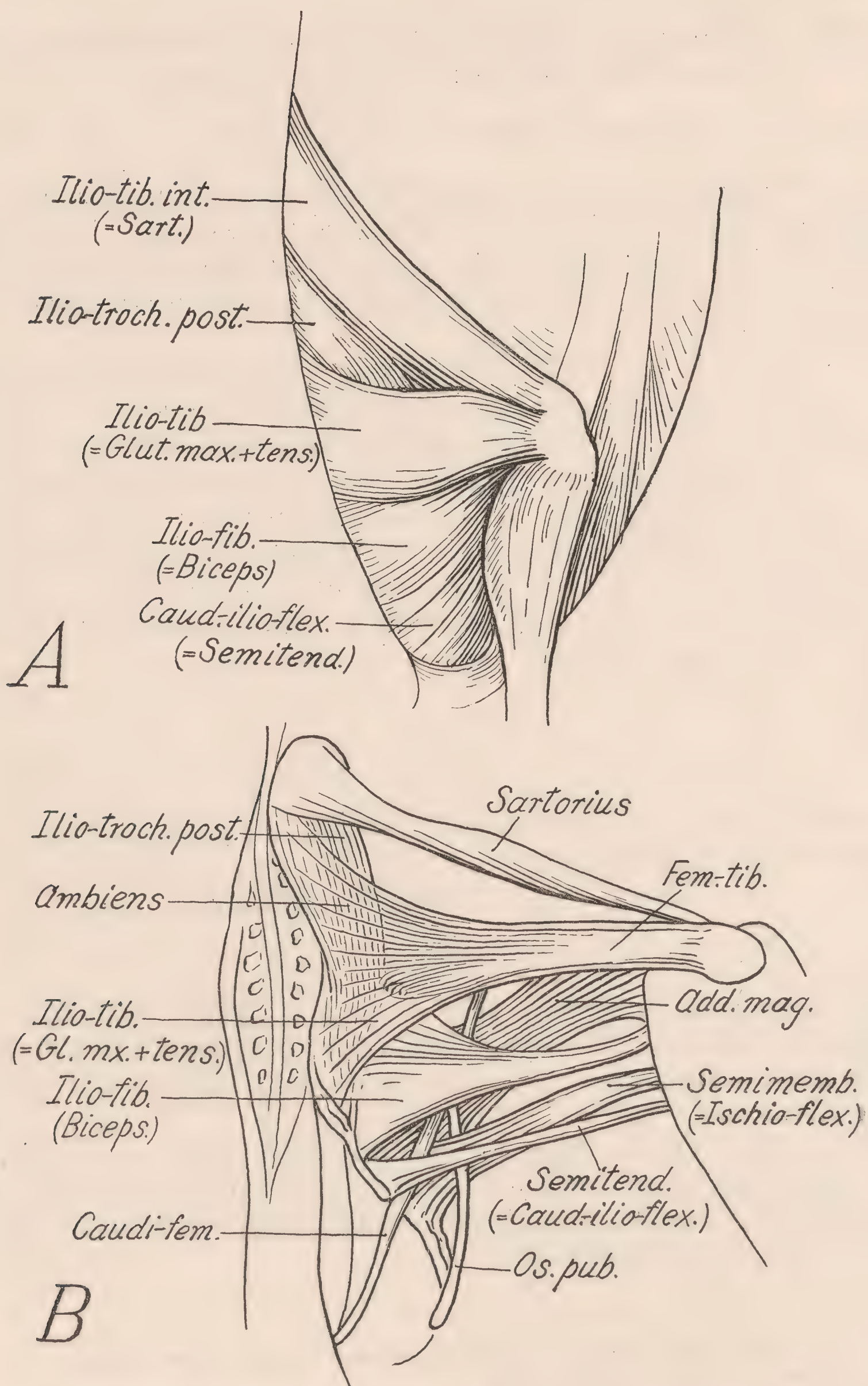


Fig. 9.

In the stegocephalian stage of quadrupedal locomotion, the short limbs were held outward from the body, the humerus and femur were very short and the feet were spreading and flat. Crawling was effected in part by a sharp downward pull of a proximal segment (humerus or femur), thus tilting the body upward on the same side and throwing the weight on the opposite foot. The long axis of the body was meanwhile thrown into alternate lateral curves, the advancing fore limb being on a convexity, the advancing hind limb on a concavity.

In the late reptilian or early mammalian stage, the feet were brought around partly under the body, the elbow and knee began to be drawn in, the scapula was rotated backward as the coracoid lost its connection with the sternum, and the body became well raised off the ground. According to a hypothesis advanced elsewhere by the writer,¹ this process was associated with the acquisition of climbing, or semi-arboreal, habits, structural vestiges of which remain in the partly divergent first digit and many other characters of early Eocene mammals.²

Two corrections should be made in the first paragraph: first, the humerus of primitive tetrapods does not pull so much directly downward as obliquely downward, forward and backward; secondly, the advancing fore limb is just in front of a convexity and the advancing hind limb just behind a concavity.

We may begin with a brief discussion of the origin and evolution of the pelvis and hind limbs in reptiles because, for reasons noted below, the evolution of the hind limbs is in some ways easier to understand than that of the fore limbs.

In the remote piscine ancestors of the tetrapod vertebrates forward locomotion was doubtless accomplished partly through lateral undulations of the body, induced by the metameric muscles and transmitted to the tail, partly through paddle-like movements of the pectoral and pelvic limbs. These limbs were the result of nodal outgrowths and subsequent concrescence of metameric muscles, nerves, and cartilages. Hence, in the earlier stages of locomotion, the movements of the paired limbs were closely correlated with, and at first subordinate to, the undulatory movements of the axial skeleton and musculature, while in the highest stages the limb movements and musculature become widely differentiated from those of the axial skeleton. At the same time the originally metameric character of the limb

Fig. 9. A. Superficial muscles of the pelvis of *Eudiptes chrysocome*. From Gadow and Selenka, after Watson.

B. Muscles of the pelvic limb of *Larus fuscus*. From Gadow and Selenka, after Selenka. Muscle names according to Gadow.

The homologies of these muscles are indicated in the table on pages 504, 505.

¹ 1910. The orders of mammals, Bull. Amer. Mus. Nat. Hist., XXVII, p. 226.

² Matthew. 1904. Arboreal ancestry of the Mammalia, Amer. Nat., XXXVIII, pp. 811-818.

muscles is progressively disguised in various degrees, some muscles, like the quadratus lumborum, pubi-ischio-femoralis internus, and caudi-ilio-femoralis of reptiles, retaining clear traces of their metameric character, while many others lose it almost entirely.

THE PELVIC LIMBS

In primitive amphibians and reptiles (cf. Pls. XLIII, XLVII) and even in dipnoan fishes the pelvis functions as a bony base located at the intersection of three main series of muscles: first, an anterior series running from the front part of the pelvis and proximal part of the limb along the backbone and flanks (here belong the sacro-spinal muscles, the quadratus lumborum, pubi-ischio-femoralis internus, and abdominal muscles); secondly, a posterior series running from the back part of the pelvis and femur along the tail (including the caudi-ilio-femoralis, caudi-femoralis, ilio-caudalis, ischio-caudalis); and, thirdly, a transverse series running outward from the pelvis to the limb both above and below the femur.

These transverse muscles running from the pelvis to the limbs are arranged in two or more concentric cones, the outer layer, running from the periphery of the pelvis to or near the knee joint, includes on the outer side the sartorius, gluteus maximus, biceps, semimembranosus, semitendinosus, etc., and on the inner side the gracilis; the deeper layers running from the deep surfaces of the pelvis to the more proximal surface of the shaft of the femur include the adductors and obturators, below the acetabulum, and the deep glutei above it. Thus in *Sphenodon* and in lizards, which retain the primitive reptilian condition, the rod-like ilia function as a fixed base, or fulcrum, between the muscles that bend the lumbar region and those that bend the tail. The muscles that run outward from the blade of the ilium to the thigh originate between and below the longitudinal muscles.

In the primitive pro-tetrapod the ventral part of the pelvis, or pubi-ischiadic plate, was doubtless of large size and strongly developed, while the ascending blade, or ilium, was small. The contact of the pelvis with the sacral rib or ribs was very loose and ligamentous. The ventral muscles, running from the under side of the femur to the outer side of the pubis and ischium, were strongly developed, as were also the muscles running from the femur backward along the tail and from the femur forward to the flanks; but the muscles running from the upper surface of the femur to the ilium were feeble. The deep gluteal muscles are specialized anterior portions of the lateral tail muscles and probably served at first rather to abduct the tail than to move either the femur or the pelvis. The superficial gluteal muscles

(ilio-tibialis) on the other hand, are derived from the obliquus abdominis externus (Gadow, 1882).

All this was related to the fact that in this stage of evolution the adaptations for preventing the body from settling down of its own weight on one side, when one foot was raised from the ground, were less perfectly developed than in later types which can raise the body far from the ground and even hold it for some time in a true standing pose. When a quadruped lifts, for example, the left hind limb off the ground, the right hind foot being firmly on the ground, the backbone and sacral region are only prevented from sagging toward the left by the action of those muscles on the right side both above and below the acetabulum which tend to pull the pelvis and backbone toward the head of the right femur. In this way, also, the sacral ribs are being forced downward and outward against the inner side of the ilium. As long as the animal remains small and the body is not raised high above the ground, especially if the connection with the sacral ribs is loose, the lifting effect can be obtained by the muscles running from the neural spines of the backbone to the top of the ilium, and from the upper border of the ilium to the knee joint, as well as by the ventral muscles running from the pubis and ischium to the femur; but, when the size becomes very great and when the body is lifted well above the ground, these muscles are reinforced by the greatly expanded gluteal mass, running from the outer surface of the ilium to the upper part of the femur. Hence, at this more advanced stage, the area on the blade of the ilium for the gluteal muscles is correspondingly expanded.

Thus the primitive reptilian ilium was probably directed backward, its posterior tip serving as a base for the powerful ilio-caudalis, its blade for the caudi-ilio-femoralis muscles. In this type of pelvis, seen in *Sphenodon*, *Varanops*, and the lizards, the thorax is usually not large and the limb bones not very stout. The space for the ilio-femoralis (deep gluteal) muscles is restricted. In heavy-bodied forms with stout limbs, on the other hand, such as *Casea*, *Moschops* (Pl. XLVII), *Cynognathus* (Pl. XLVI), and *Dicynodon*, the blade of the ilium expands anteriorly, greatly increasing the areas for the deep gluteal (ilio-femoralis) muscles. This anteroposterior expansion of the ilium culminates in the birds and dinosaurs, which have correspondingly extended gluteal muscles, for preventing the sagging of the body, as well as for moving the opposite femora.

In *Cynognathus* the expansion and forward extension of the gluteal surface was well advanced, but the subsequent narrowing of the ilium, which is so characteristic of the ilium of primitive mammals, had not yet supervened.

In fully aquatic reptiles, on the other hand, the weight of the body being

largely buoyed by the water, there is less need for counteracting the tendency to sag on one side when the femur of that side is raised. Hence, in the more specialized aquatic reptiles, that is those that swim chiefly by means of the tail rather than of the limbs, the muscles that tend to press the pelvis and backbone against the femur are small or more or less reduced. Thus we have an adaptational reason both for the reduction of the ilia and loosening of the sacrum in fully aquatic types and for the opposite expansion of the ilium and extension of the sacrum in animals that hold the body well raised from the ground.

In forward locomotion, both on the ground and in swimming, the pelvis as a whole is turned from side to side and rocked in a transverse plane. There is always a special cooperation of groups of muscles of the opposite sides: on one side above the acetabulum, on the other side below it, and on one side in front and on the other side behind it. For example, some of the inferred movements of the pelvis and femora of a reptile may be considered, beginning at the moment when the left hind limb is directed backward as far as possible and the right hind limb is directed forward, both hind feet being on the ground. At this moment on the left side a group of muscles running from the left femur backward to the ischium and to the tail and from the left ilium and ischium to the tail are in a state of maximum tension, while on the right side the corresponding sets of muscles are relaxed. The resulting tendency to turn the pelvis toward the left is probably reinforced by the tension of muscles on the right side lying in front of the pelvis, such as the *quadratus lumborum*, *ilio-costalis*, and *obliquus abdominis*. But, at the same time the pelvis has also been tilted vertically toward the left side, through the tension of the right ventral muscles running from the under side of the pelvis to the femur and of the left dorsal muscles running from the left ilium to the femur, as well as from the thrust of the left femur.

In reptiles which are able to straighten fully the knee joints (the primitive Permian types had permanently crooked knee joints) the turning of the pelvis toward the left is probably checked and the opposite movement begun by the thrust of the left femur upon the acetabulum, due to the straightening of the left knee joint at the end of the backward stroke of the left hind limb. This tends to push the pelvis toward the right. The left femur is then drawn forward, the right femur backward, the whole pelvis and sacrum meanwhile turning from left to right upon the articular facets of the posterior lumbar and anterior caudal vertebræ. The powerful *caudi-femoralis* and *caudi-ilio-femoralis* muscles serve not only to vibrate the tail but alternately to check and reinforce the muscles that draw the opposite femora forward and backward.

In primitive mammals the ilium has grown forward in front of the ace-

tabulum and the pubis and ischium have been prolonged behind and below it. In this way the gluteal muscles above the femur and the obturators and adductors below the femur by an extension of function serve not only to twist the pelvis and to prevent collapse when one limb is lifted but also to draw the femora more directly backward and forward. This is associated with a progressive forward turning of the femur, so as to bring the knees in toward the flanks and the feet nearer to the mid line. In the highly specialized graviportal mammals, which have straightened the limbs at the knee-joint so as to transmit the weight more directly through the post-like limbs, the blade of the ilium has become expanded in a nearly transverse direction and at right angles to its original position. In these forms, again, the expanded gluteal and iliac muscles function as much to overcome the tendency to collapse when one foot is raised from the ground as to move the femur of the advancing limb. In man, also, a similar transverse expansion of the ilium with a correlated expansion of the gluteus maximus serves a similar purpose.

The foregoing transformation of the primitive reptilian pelvis into the specialized mammalian types has been accompanied by a marked differentiation of a great muscle mass known as the pubi-ischio-femoralis internus, which originates on the inner-upper surface of the pubis and ischium and beneath the sacral vertebræ and, passing forward over the anterior rim of the pubis and running backward, is inserted usually on the upper part of the femur. The dorsal portion of this mass, in the mammals, extends upward and forward along with the forwardly growing ilium and gives rise to the iliacus and psoas muscles, which powerfully aid in pulling the femur forward and inward. The tail muscles of typical mammals, on the other hand, lose much of their locomotive function, the tail becoming sharply constricted from the body and the caudi-femoralis and caudi-ilio-femoralis reduced and broken up into fragments such as the caudi-femoralis and the pyriformis. Thus the pubis and ischium of mammals finally came to lie chiefly behind the acetabulum, and the adductors and obturators tend to pull the femur backward as well as inward.

In birds, also, the ilium (Pl. XLVI) has grown forward, producing a corresponding extension of the gluteal areas, while the pubis and ischium also have been produced behind the acetabulum. The pubis, however, has become variously reduced, because the pubi-ischio-femoralis externus and related muscles now find their principal attachment on the ischium and the pubis and ischium are both bent backward in order to draw the femur backward as much as inward.

In the ornithischian dinosaurs the expanded prepubic process appears to have served as a base for a forward extension of the pubi-ischio-femoralis

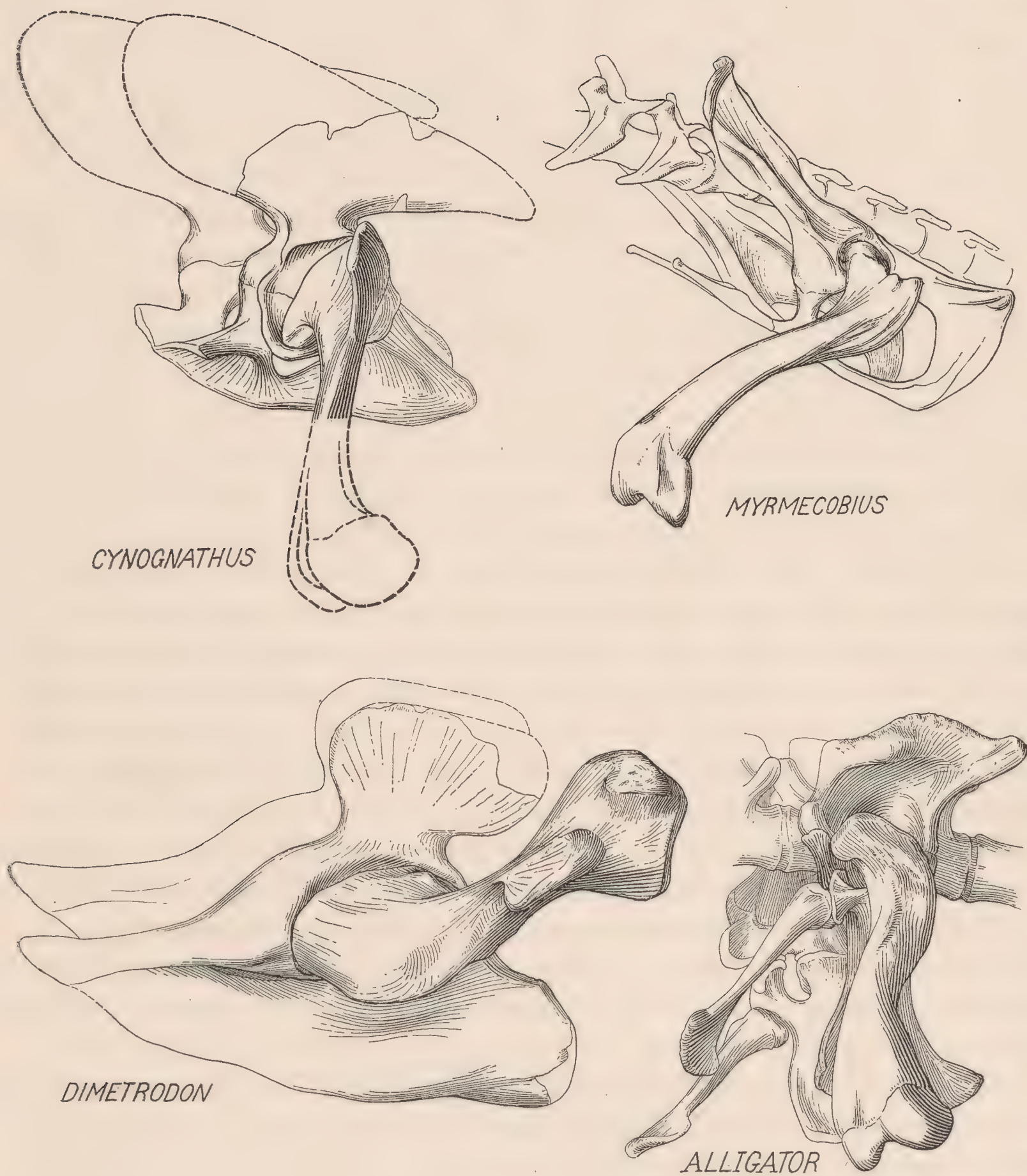


Fig. 1 .

Fig. 10. Form and relations of the pelvis and femur in a primitive reptile and in higher types.

Dimetrodon gigas, Permian of Texas. Pelvis and femur adapted for sprawling gait with sharply bent knees and pes turned partly backward, these characters being also associated with great thickness and strength of the tail. The ilium is chiefly above and behind the wide acetabulum; the pubis is produced in front of it; the wide pubi-ischiadic plate is not fenestrated; the femur was usually directed outward, upward and backward.

Alligator, modernized reptile. Pelvis and femur adapted partly for sprawling gait, partly for running or leaping with body well raised from the ground. Femur can be turned forward, outward and downward. Tail thick and powerful. Pubi-ischiadic plate widely fenestrated; pubis excluded from acetabulum.

Cynognathus, progressive therapsid reptile from the Trias of South Africa. Pelvis and femur intermediate between the primitive reptilian and primitive mammalian stages. Ilium produced in front of acetabulum, pubi-ischiadic fenestra of moderate size. The femur could be directed forward, outward and downward and the body well raised from the ground. Femur with large external trochanter for the attachment of the deep gluteal muscles.

Myrmecobius, a primitive existing mammal. Pelvis and femur adapted for running, with the body well raised off the ground and the knees brought forward near the flanks, the feet being placed well under the body. Ilium widely produced in front of acetabulum and with reduced caudal process, pubis and ischium well fenestrated produced behind acetabulum; femur with large external trochanter.

externus and internus and perhaps also for the ambiens. The quadratus lumborum may have passed above it to be inserted on the femur. In any case, the muscles carried by the prepubic process very probably served both to draw the femur forward and, as adductors, to assist the gluteal muscles in preventing the body from collapsing when the opposite limb was lifted.

In *Cynognathus* the postacetabular region of the pubi-ischiadic plate is more extended than the pre-acetabular part, so that there was some approach to the conditions seen in monotremes.

The acetabulum in primitive reptiles is very large and, being widely open on all sides, it permits the flattened oval head of the femur to assume many different positions. The primitive acetabulum is more or less three-sided, with a wide cotyloid notch at the base. Ligaments, perhaps corresponding to the ligamentum teres, are extended across this notch. The three elements of the pelvis meet in the center of the acetabulum in a triradiate suture, perhaps because this triradiate growth tract is farthest removed from the rigid centers of ossification of the three elements which are above, below, and behind the femur, respectively, each one being placed between opposing sets of muscle pulls. The primitive acetabulum is closed at the bottom but in crocodiles, dinosaurs, birds, and one of the monotremes (*Echidna*) the deepest part of the acetabulum becomes fenestrated. In these cases the open part is covered in life with heavy ligaments, which are probably as strong as the bones themselves.

The thyroid fenestra is analogous with other fenestræ in the skeleton, such as those in the temporal region or that lying between the clavicle and the epicoracoid. In such cases the fenestration appears at the middle part of an insertion area, the borders of the area becoming greatly strengthened. The fenestrated area apparently permits a free expansion and contraction of the muscles, as may be clearly seen in the temporal fenestræ of *Sphenodon*. In *Cynognathus* and other Therapsida the small pubi-ischiadic openings had apparently not yet extended to the mid line and were more comparable with true obturator foramina than with the true thyroid fenestræ of reptiles (Williston).

In Crocodilia and Saurischia the pubis and ischium are prolonged downward below their primitive level, so that in the alligator there is a deep cleft in the muscle masses between the pubis and the ischium. The same was doubtless true of the Saurischian dinosaurs.

The action and pose of the hind limbs in forward locomotion is naturally dependent not only upon the formation and arrangement of the parts of the pelvis and of the pelvic musculature but also upon the form of the femur. In this connection a study of the head of the femur and of the homologies of the various trochanters of reptiles, birds, and mammals has become

necessary (see Part IV below). From this it is seen that the great development of the external or great trochanter of the femur in *Cynognathus* and mammals is correlated with the expansion of the gluteal surface of the ilium, that the primitive internal trochanteric crest gave rise through divergent evolution, on the one hand, to the lesser trochanter of mammals and, on the other hand, to the fourth trochanter of dinosaurs and birds. The primitive internal trochanter gave attachment to the muscles that draw the femur directly inward toward the pelvis and backward toward the tail. In the fourth trochanter the latter set are the most concerned while the lesser trochanter of mammals gives insertion to muscles that draw the femur forward and inward (iliopsoas, pectineus).

THE PECTORAL LIMBS

The fore limb of primitive vertebrates presents many analogies in structure and function with the hind limb. Just as in the hind limbs, there is a set of muscles running from the vertical blade of the girdle posteriorly to the side of the body, another set running from the girdle anteriorly toward the head, and a third set running transversely from the girdle to the proximal limb element both above and below the fulcrum. The chief differences between the fore and hind limb arise from the fact that the pectoral girdle in the piscine stage of evolution was originally attached to the occiput and was associated with the opercular region almost as much as with the pectoral limb itself. The main vertical dermal element, or cleithrum, in fishes is concave anteriorly, conforming to the curve of the opercular region while the true clavicular plate ("infraclavicle") projects forward beneath the throat. Even in the higher vertebrates the dorsal muscle mass (trapezius) is innervated by the spinal accessory nerves, this fact indicating that it once was located near the occiput. The underlying cartilaginous girdle in fishes rarely has a prominent dorsal branch, its scapular portion being usually short (except in the sturgeon and its allies). The ventral, or coracoid, portion of primitive fishes is, on the contrary, of great functional importance and the anterior process of the coracoid extends forward and downward to the mid line. The glenoid region in fishes is placed at the junction of the scapula and the coracoid and faces posteroexternally, just as it does in primitive tetrapods. The muscles of the pectoral fins in the lowest types of fishes still show their metameric derivation but in the higher fishes especially in dipnoans and crossopterygians, extensive concrescence and outgrowth of neural and muscular segments has already taken place. There are muscles for raising (abducting), depressing, protracting, retracting, twisting, and spreading the fins but, as yet, it is difficult to homologize these

in any detail with the limb muscles of tetrapods, although Humphrey (1872) has analyzed the pectoral and pelvic muscles of tetrapods into layers corresponding with similar layers in fishes.¹

When the ancestral tetrapods emerged from fishes and the opercular region became highly modified the cleithrum, which had been the most important dermal element in the fishes, became rapidly reduced, although in the earliest amphibians of the Carboniferous this element was still of considerable size. At the same time the scapular portion of the cartilaginous girdle became greatly developed and finally replaced the cleithrum in functional importance. Meanwhile the pectoral girdle became freed from the skull through the loss of the posttemporal element and the progressive differentiation of the neck. These changes were, no doubt, accompanied by corresponding modifications of the muscles; those running from the scapula to the humerus and the muscles for flexing and extending the limbs becoming greatly enlarged.

Primitive tetrapods still retain much of the piscine mode of undulation of the body in forward progression. This is accomplished partly by the axial musculature and partly through the action of the longitudinal muscles running along the side of the neck to the scapula and from the scapula back to the ribs. Since the opposite scapulocoracoids articulate movably with the sternum and are braced by the powerful interclavicles and clavicles, the pectoral arch and sternum move first as a whole and, secondly, the scapulocoracoids may slip back and forth on the sternum. The sternum forms a sort of shield or box for the pericardium and adjacent structures, as well as a base for the powerful pectoral muscles. The lateral movement of the pectoral arch and sternum as a whole takes place at the ribs, which move more or less freely at the junction of the cartilaginous ribs with the dermal ventral ribs, or gastralia.

The forward turning of the right side of the pectoral girdle and the synchronous backward movement of the left side in primitive reptiles seems to be accomplished somewhat as follows: The right levators of the scapulæ (Figs. 1, 2) and the omotrachelian contract and cooperate with the left serratus superficialis and serratus anterior profundus. This twists the pectoral girdle toward the right. A rocking movement in a transverse vertical plane might be accomplished through the cooperation of the right trapezius with the left pectoralis and coracoid muscles, and especially with the left subscapularis and serratus profundus. The movement toward the right is also assisted by the extension backward of the right fore limb, pushing the right

¹ Watson. *Journ. Anat.*, 1917, p. 61, has recently put forward some interesting opinions on the derivation of the muscles of the forearm in the earliest tetrapods.

humerus forward and upward against the glenoid. The opposite movement is, of course, then initiated through the sudden relaxation of the above named muscles. The left levators and omotrachelian then pull the left scapula forward and the right serrati pull the right scapula backward.

As a result of this lateral undulation of the shoulder-girdle and of the slipping of the coraco-scapula upon the sternum, the reach of the fore limb on each side is correspondingly increased. In this way the fore limbs cooperate with the hind limbs in throwing the long axis of the body into alternate curves, the right fore limb being fully extended forward at the same time that the right hind limb is extended backward and vice versa.

Cynognathus had already lost the cleithrum but, as it retained the primitive interclavicle and as the scapula was fastened both to the sternum and to the clavicle, the general movement of the shoulder-girdle was, no doubt, as described above. When the shoulder-girdle was momentarily fixed by one limb holding fast to the ground the massive levators and omotrachelian would doubtless have assisted in moving the heavy head and neck. This mode of action of the pectoral musculature is retained in the monotremes, which have the opposite scapulocoracoids articulated with the sternum and the superficial neck muscles very heavy. In typical mammals, however, through the freeing of the coracoid from the sternum the whole girdle acquires great mobility with reference to the trunk and the undulating motion of the body is much less conspicuous.

In reptiles and primitive mammals the fore and hind limbs cooperate with each other in the following way: the fore and hind limbs of the same side move in opposite directions; on the other hand the right fore limb moves in the same direction with the left hind limb and vice versa. The backwardly extended fore foot is raised and moved forward immediately before the forwardly extended hind foot touches the ground. This criss-cross movement of the limbs is correlated with alternate lateral bendings and twistings of the thorax, and with corresponding turning and twisting of the girdles, in such a way that the forward and backward reach of the divergent limbs on one side are increased while the convergent limbs of the opposite side are brought still nearer together. Another advantage of this arrangement is that the pull and push of the limb muscles is supplemented by the powerful spiral and spring-like action of the axial musculature, while a third advantage is that by stretching the limbs of the same side in opposite directions the forward thrusts and pulls are brought nearer to the mid line, and thus the speed is increased. Hence, it should and does follow that the faster a reptile moves the narrower is its trackway.

PART IV.—NOTE ON THE MORPHOLOGY AND EVOLUTION OF THE
FEMORAL TROCHANTERS IN REPTILES AND MAMMALS

By W. K. GREGORY.

In studying the pelvis and femur of *Cynognathus*, *Moschops* and other Therapsida I was led into a review of the morphology of the head of the femur and of the various trochanters. The following series of vertebrates were studied in this connection:

TEMNOSPONDYLI

†*Eryops*

URODELA

**Cryptobranchus*

**Necturus*

ANURA

**Bufo*

COTYLOSAURIA

†*Diadectes*

†*Seymouria*

†*Propappus*

PELYCOSAURIA

†*Dimetrodon*

Ophiacodon

Varanops

Theropleura

CASEASAURIA

†*Casea*

THERAPSIDA

†*Elurosauros*

Endothiodon

†*Moschops*

†*Cynognathus*

†*Diademodon*

Dicynodon

RHYNCHOCEPHALIA

**Sphenodon*

CHELONIA

**Testudo*

SQUAMATA

†*Varanus*

**Iguana*

Heloderma

Chamaeleo

PELYCOSIMIA

†*Erythrosuchus*

PSEUDOSUCHIA

Aëtosaurus

Ornithosuchus

Thecodontosuchus

PARASUCHIA

Typothorax

†*Mystriosuchus*

†*Acompsosaurus*

CROCODILIA

Geosaurus

Dacosaurus

**Alligator*

THEROPODA

†*Plateosaurus*

Sellosaurus

Anchisaurus

†*Ornitholestes*

†*Struthiomimus*

†*Allosaurus*

†*Tyrannosaurus*

SAUROPODA

Haplocanthosaurus

†*Camarasaurus*

†*Brontosaurus*

†*Diplodocus*

ORNITHISCHIA

†*Iguanodon*

†*Camptosaurus*

†*Trachodon*

Corythosaurus

†*Thescelosaurus*

†*Monoclonius*

Stegosaurus

†*Ankylosaurus*

MARINE REPTILES

Tylosaurus

† <i>Cryptocleidus</i>	† <i>Myrmecobius</i>
<i>Ichthyosaurus</i>	† <i>Phalangista</i>
SAURURÆ	† <i>Phascolumys</i>
<i>Archæopteryx</i>	* <i>Hypsiprymnodon</i>
ODONTORNITHES	* <i>Macropus</i>
† <i>Hesperornis</i>	CARNIVORA
APTERYGIFORMES	† <i>Patriofelis</i>
* <i>Apteryx</i>	† <i>Hyænodon</i>
STRUTHIIFORMES	† <i>Pachyæna</i>
* <i>Struthio</i>	* <i>Felis</i>
CASUARIFORMES	PRIMATES
† <i>Dinornis</i>	* <i>Lemur</i>
DIATRYMÆ	* <i>Homo</i>
<i>Diatryma</i>	PERISSODACTYLA
GALLIFORMES	* <i>Tapirus</i>
<i>Gallus</i>	* <i>Equus</i>
ANSERIFORMES	* <i>Rhinoceros</i>
<i>Cygnus</i>	† <i>Palæosyops</i>
<i>Anas</i>	† <i>Brontotherium</i>
COCCYGES	PROBOSCIDEA
† <i>Geococcyx</i>	† <i>Mastodon</i>
MONOTREMATA	* <i>Elephas</i>
* <i>Echidna</i>	AMBLYPODA
* <i>Ornithorhynchus</i>	<i>Pantolambda</i>
MARSUPIALIA	† <i>Coryphodon</i>
† <i>Didelphys</i>	† <i>Uintatherium</i>

In the recent forms marked * the femoro-pelvic muscles have been considered in their relations with the bony elements, partly by "autoptic examination" of alcoholic specimens, partly by study of the dissections figured in the literature. In the recent and fossil forms marked † the bony elements alone have been examined, but with special reference to the probable origin, insertion, and function of certain femoro-pelvic muscles. In the remaining genera listed, as well as in many others not listed, the bones were examined but revealed little or nothing that had not already been noted in other genera.

The various trochanters have been tentatively homologized by direct comparison of the different genera and these tentative homologies were, so far as possible, confirmed by reference to the musculature of these parts in recent reptiles.

A.—OSTEOLOGICAL EVIDENCE

The head of the femur in all recent reptiles and in the great majority of fossil reptiles occupies the whole proximal end of the femur. It is widely oval in section, is located directly on the top of the shaft, instead of being

set off to one side as in mammals and birds, and is not separated from the shaft by a neck. The whole head could be thrust into the acetabulum when the femur was directed outward, as in primitive sprawling types; but when the femur is directed forward the outer part of the head protrudes from the acetabulum.

The "medial trochanter" (internal trochanteric crest) of Permian reptiles (Pl. XLVIII) appears to have been shifted either down the shaft to give rise to the "fourth trochanter" or up the shaft, as in lizards and turtles, to give rise to the lesser trochanter. Von Huene (1911, pp. 55-56) has noted that the medial trochanter of Permian and Triassic reptiles is homologous with the fourth trochanter of later types and Professor Williston informs the writer that he came to the same conclusion, which was also reached independently by the writer.

The trochanteric eminence on the under side of the femur of crocodiles, alligators, phytosaurs, and *Erythrosuchus* (Fig. 11), has every appearance of homology, on the one hand, with the medial trochanter of Permian types and, on the other hand, with the "fourth trochanter" of *Plateosaurus*, *Sellosaurus*, Theropoda, Ornithischia, and the birds. Dollo (1883) contrasted the femora of *Iguanodon* and of birds, on the one hand, with that of the crocodile, on the other, concluding that the femoral musculature of *Iguanodon* was more bird-like than reptilian. He left the medial trochanter of the crocodile unnamed and undefined, but direct comparison of the crocodile femur with that of a mounted *Trachodon* skeleton strengthens this probable homology. In another direction, the crocodile trochanter compares closely with those of *Typothorax*, *Plateosaurus*, and *Sellosaurus*, and these connect surely with the theropod and sauropod types. Again, direct comparison of the femora of *Allosaurus* and *Brontosaurus* with each other and with *Trachodon* bears out the apparent homology of the fourth trochanter in all.

In the therapsid-mammal series perhaps the most primitive femur examined was that of *Ælurosaurus* (Pl. XLVIII). The general form of the femur is almost typically reptilian. The widely oval head occupies the whole proximal end of the curved shaft, as in crocodiles, lizards, and primitive Permian reptiles. The latero-superior margin of the femur, near the proximal end, is raised into a wide swelling, which is apparently homologous with the great trochanter. The slight emargination between the head and the great trochanter represents the neck of the femur of mammals. On the medial surface of the femur is a long ridge, possibly homologous with the pectineal line of mammals but not ending above in a definite tubercle.

In the deinocephalian *Moschops* (Pls. XLVII, XLVIII) the head is excessively prolonged outward into a thin articular ridge, called the "trochanteric ridge" by Watson but regarded by the writer as part of the head;

the great trochanter itself is apparently represented by a low swelling on the outer side of the shaft. There is little, if any, trace of the medial ridge and trochanter. In *Dicynodon* the condition is essentially similar to that in *Ælurosaurus* save that the medial ridge is short and shifted to the medial border of the femur, in the position of a lesser trochanter.

In *Cynognathus* (Pl. XLVIII) we have a distinct approach to the mammalian condition. The widely oval head is becoming separated by an incipient notch, or neck, from the much enlarged and protruding great tro-

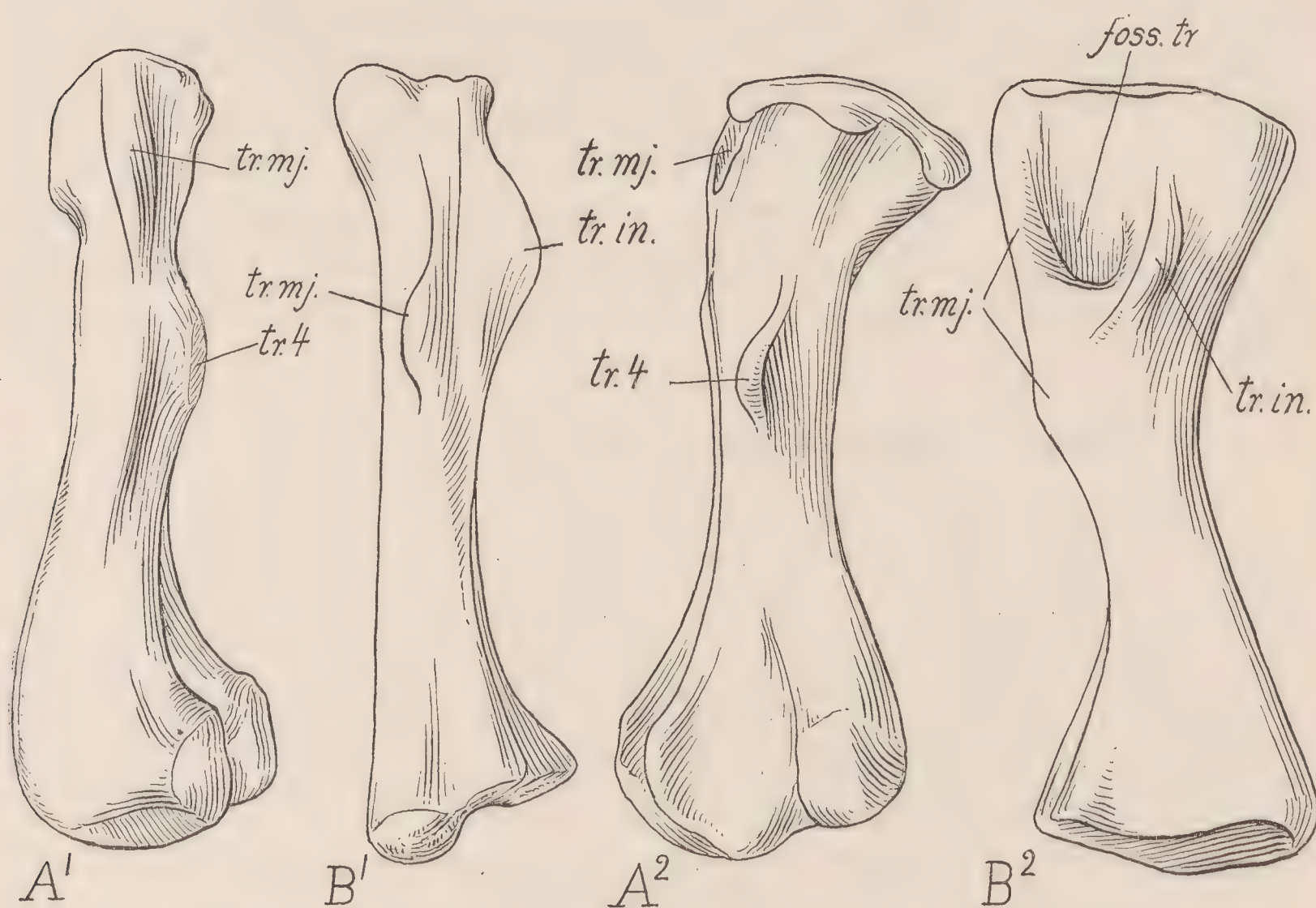


Fig. 11. Comparison of the femora of two early diapsid reptiles, indicating the probable homology of the "fourth trochanter" with the internal trochanter of primitive reptiles.

A¹. *Typothorax coccinarum* Cope, Trias, New Mexico. Order Parasuchia or Pseudosuchia? Left femur, lateral aspect. Adapted from von Huene 1915.

Fourth trochanter clearly homologous with that of dinosaurs and with the internal trochanter of Crocodilia.

B¹. *Erythrosuchus africanus* Broom, Trias, South Africa. Order Pelycosimia. Left femur lateral aspect. Adapted from von Huene 1911.

Internal trochanter evidently homologous with that of Permian reptiles but in the way to assume the form and position of a fourth trochanter.

A². *Typothorax coccinarum*. Left femur, posterior or caudal aspect. Adapted from von Huene 1915.

B². *Erythrosuchus africanus*. Left femur, posterior aspect. Adapted from von Huene 1911.

chanter. The medial ridge, near the medial border of the femur, is sharply defined and terminates above in a low eminence, which Seeley and Broom recognized as the homologue of the lesser trochanter of mammals. The third trochanter is not differentiated.

B.—EVIDENCE FROM THE MUSCULATURE

The evolution and morphology of the femoral trochanters are elucidated by a study of the functions of the muscle attachments and movements of the femur and of the pelvis. From Gadow's very complete descriptions of the limb muscles of recent reptiles the writer compiled lists of the origins, insertions, and directions of the muscles that move the femur in lizards, crocodilia, *Sphenodon*, and *Testudo*, and from this list, supplemented by examination of alcoholic specimens, it was found that the muscles could be conveniently grouped under four sets, with reference to the direction of movements of the femur (omitting the rolling or twisting movements), as follows:

1.—Muscles Tending to Draw the Femur Forward and Inward

a) *Quadratus lumborum*. In the alligator (Pl. XLIII) this muscle is attached on the upper third of the femur on the antero-dorsal surface. A powerful muscle connecting the axial and the appendicular systems.

b) *Pubi-ischio-femoralis internus* (Pl. XLIII). Running from the dorsal surface of the pubis and around its anterior borders, turning backward and inserted on or below the internal trochanter of the femur. For reasons which are discussed elsewhere in these papers, this group (pubi-ischio-femoralis internus) is believed to have given rise to the ilio-psoas + pectineus of mammals and is attached on or near or below the lesser trochanter (trochanter minor).

2.—Muscles Tending to Draw the Femur Chiefly Backward toward the Tail

a) *Caudi-femoralis* (Pl. XLIII). Attached to the back of the femur, either to the internal (fourth) trochanter or back of the external trochanter.

b) *Caudi-ilio-femoralis* (Pl. XLIII). Attached to the femur, either on the outer surface near the external trochanter (*Sphenodon*, Crocodilia) or on the posterior surface (Sauria), or on both trochanters and on the fossa trochanterica (Chelonia).

c) *Pubi-ischio-femoralis posterior* (Pls. XLIII, XLVI). Arises chiefly from the posterior region of the ischium and is inserted on the posterior region of the ischium and is inserted on the posterior surface of the femur, either in the trochanteric fossa (Sauria), or on the external trochanter (*Sphenodon*), or on the posterior surface of the femur from the internal

trochanter down nearly to the condyles (Crocodilia). This muscle is probably homologous with the so-called "ischiofemoralis" of birds,¹ which is inserted on the crest *above* the fourth trochanter. It is also probably homologous with the obturator internus and associated muscles of mammals, which are inserted in or near the digital fossa.

3.—Muscles Tending to Draw the Femur Inward or Inward and Backward Toward the Pelvis

a) *Pubi-ischio-femoralis externus* (Pl. XLIII, XLV, XLVI). Arising from the outer surface of the pubi-ischiadic plate and inserted in the region of the trochanteric fossa and often on the internal trochanter. This muscle is probably homologous with the obturator externus of mammals, which is inserted in the trochanteric, or digital, fossa.

b) *Ischio-femoralis* (Gadow) (Pls. XLIII, XLVI). Inserts on the posteromedial surface of the femur below the trochanter. Probably homologous with the adductor muscles of mammals.

4.—Muscles Tending to Extend and Abduct the Femur (i. e. to Draw it Upward toward the Ilium)

a) *Ilio-tibialis* I (= *Glutæus maximus*). Pl. XLIII.

b) *Ilio-tibialis* II (= *Sartorius*). Pl. XLIII.

c) *Ilio-femoralis* (= *Glutæus medius* + *minimus*). Pl. XLIII. Inserted on the external trochanter or on the outer border of femur.

d) *Ambiens* (= *Rectus femoris*). Pls. XLIII, XLVII.

CONCLUSIONS

From the foregoing analysis we may define the trochanteric fossa and extend and revise the definitions of the several trochanters given by Dollo.

Trochanteric Fossa (Pl. XLVIII)

(= Digital fossa of mammals)

A more or less V-shaped area on the medial surface of the femur, usually near the proximal end. Bounded originally chiefly by the external and internal trochanteric crests. Originally this fossa may have given insertion to the following muscles:

(a) *Pubi-ischio-femoralis externus* (= obturator externus). Partly on internal trochanter.

(b) *Pubi-ischio-femoralis posterior* (= obturator internus, gemelli + quadratus femoris).

¹ See table on p. 505.

(c) *Caudi-femoralis*. May have been attached around the borders of the trochanteric fossa, extending below it on the medial surface of the shaft.

(d) *Caudi-ilio-femoralis*. Perhaps more on outer margin of fossa.

In mammals groups *a* and *b* are still inserted in the trochanteric (digital) fossa; *c* and *d* are no longer associated with it.

External Trochanter (Pl. XLVIII)

(= Trochanter major, great trochanter, of mammals)

Arising primarily from the outer border of the shaft towards the proximal end, giving insertion on its outer border to the *ilio-femoralis*, posteriorly to part of the *caudi-ilio-femoralis*. On its posterior surface the region of the great trochanter sometimes gives insertion also to the *caudi-femoralis*. The great trochanter in most reptiles (including the Sauropoda) remains on the outer side of the shaft more or less near the proximal end. The outer portion of the head itself has sometimes been wrongly called "great trochanter," especially in the femur of Sauropoda.¹

Internal Trochanter (Pl. XLVIII)

(= Trochanter minor, tr. medialis, lesser trochanter)

Giving insertion especially to the *pubi-ischio-femoralis internus*, which gives rise to the iliopsoas + pectineus, which tends to pull the femur forward. Other muscles more or less closely associated with the internal trochanter are the *pubi-ischio-femoralis externus* (= obturator externus), and the adductors (*pubi-ischio-femoralis posterior*).

Fourth Trochanter (Pl. XLVIII and Fig. 11)

(Of birds, dinosaurs, phytosaurs, etc.)

Represents the middle and lower parts of the primitive internal trochanteric crest. Present in crocodilia, phytosaurs, etc., dinosaurs and birds.

Together with the crest above it, it gives insertion especially to

caudi-femoralis (part I)

ischio-femoralis (= adductors)

pubi-ischio-femoralis posterior (= obturator internus).

The lesser trochanter of mammals and the fourth trochanter of birds and dinosaurs are therefore divergent derivatives of the internal trochanter

¹ The writer inclines to the opinion that in the ornithischian dinosaurs the proximal surface of the so-called great trochanter was covered by a bursa, as is the similar smooth surface above the great trochanter in the Ostrich (Garrod and F. Darwin, 1872); and that the gluteal muscles were attached on the outer side of the great trochanter and not upon its top.

of primitive reptiles. The lesser trochanter of mammals, representing the upper or proximal part of the primitive trochanteric crest, points forward and is associated especially with the pubi-ischio-femoralis internus (= ilio-psoas + pectineus). The fourth trochanter, derived from the distal part of the primitive trochanteric crest, points backward and is associated especially with the ischio-femoralis, pubi-ischio-femoralis posterior and caudi-femoralis (part I).

Third Trochanter (Pl. XLVIII, *Pachyæna*)

(Of primitive placental mammals)

Apparently represents a new attachment of the ilio-tibialis, part II, (= glutæus maximus) which originally ran to the tibia, as it does in reptiles and monotremes.

The following table summarizes the relations of the several trochanters to the muscles and the probable homologies of the latter.

	SPHENODON	ALLIGATOR	MONOTREME	PLACENTAL
Muscle	Ilio-femoralis	Ilio-fem.	{ Gluteus minimus Gluteus medius	{ Gluteus minimus Gluteus medius
Insertion	Latero-sup. border of femur	The same	Trochanter major	Trochanter major
Muscle	Ilio-tibialis	Ilio-tibialis ext.	Gluteus maximus	{ Gluteus max. Agitator caudæ
Insertion	Head of tibia	On tibia	Tibia and fibula	3rd trochanter (glut. max.)
Muscle	Pubi-ischio-fem. int.	The same	{ Pectineus (c) Iliacus (b) Psoas major (a)	Pectineus Iliacus Psoas major
Insertion	On medial trochanter	Near and on medial trochanter	Insertion: (a) on troch. minor (b) near " (c) below "	The same

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PART V.—A RECONSTRUCTION OF THE SKELETON OF *CYNOGNATHUS*

BY W. K. GREGORY AND C. L. CAMP

The partial skeleton of *Cynognathus crateronotus* described by Seeley (1895) included, besides the almost perfect skull and mandible, a nearly complete backbone (except for the tail, which was represented by only a few of the proximal caudals), a well preserved scapulocoracoid, the greater part of the pelvis, and the proximal parts of the humerus and femur. Casts of these parts, supplied by the British Museum, have been used in the present studies, together with fragments of the girdles and limb bones of *Cynognathus* in the Broom collection of this Museum.

The subordinal characters of the missing parts of the limbs were probably not very dissimilar to those of "*Microgomphodon*" *eumerus* (Fig. 12) as described and figured by Seeley. According to Watson this skeleton probably represents a small cynognathid, and the very peculiar character

Fig. 12. *Microgomphodon eumerus* Seeley (small cynognathid, Watson), Trias, South Africa. Natural size. After Seeley 1895.

Part of skeleton, showing ventral aspect of hinder part of vertebral column, pelvis, and hind limb.

E. Posterior part of the dorsal region showing the eleventh (?), twelfth (?) and thirteenth (?) ribs (cf. Fig. 13, A).

C. Lower dorsal, lumbar and sacral regions, with the pelvis and left hind limb.

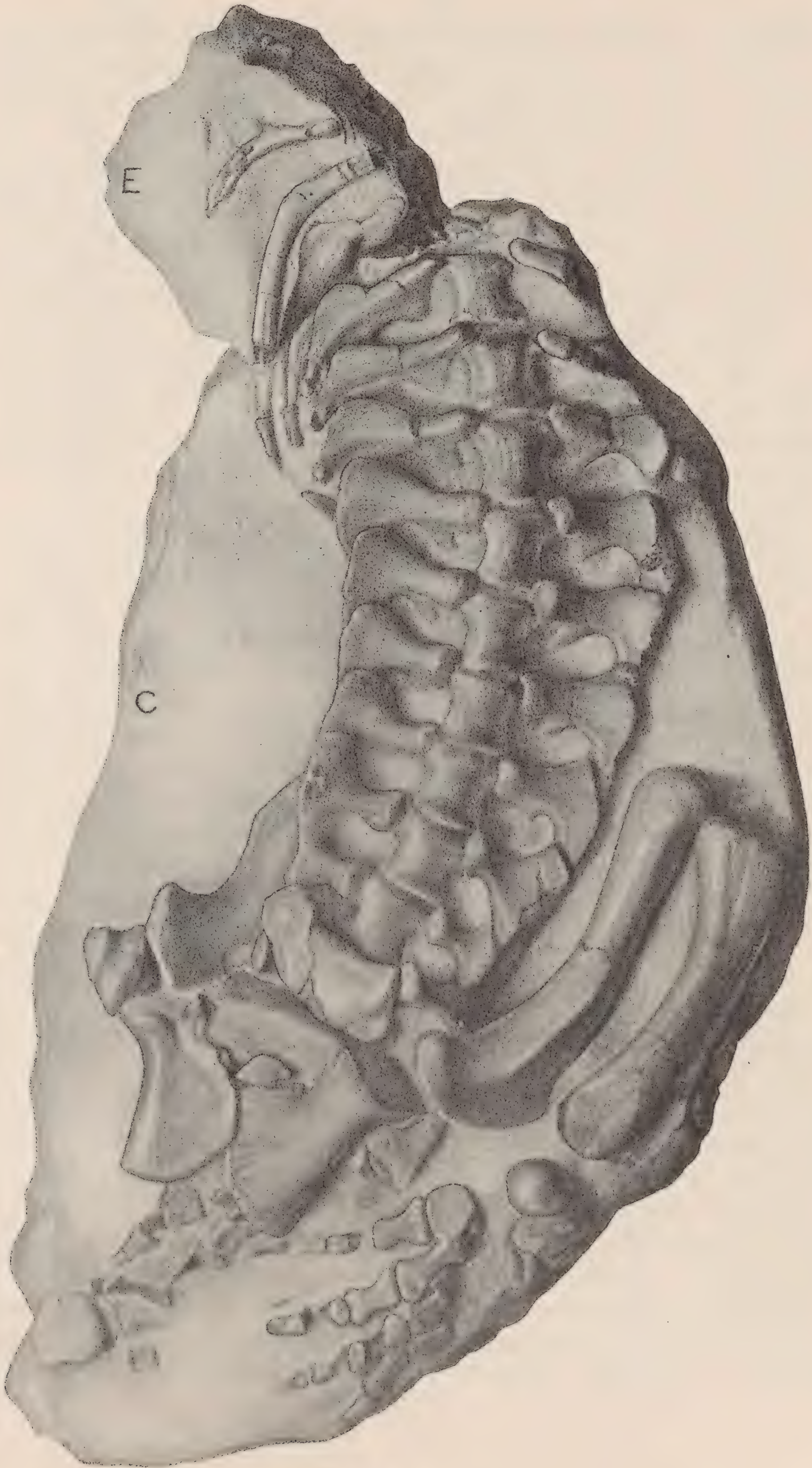


Fig. 12.

of the lumbar and lower dorsal ribs which it shares with *Cynognathus* indicates that the rest of the skeleton must be fundamentally similar. As the greater part of the manus and pes is preserved in this animal, it probably gives us a fair idea of the character of the feet of *Cynognathus*, except as to size and proportions. The femur of *Tribolodon* Seeley and the femur of *Diademodon* described by Broom doubtless supply a general idea of the form of the distal end of the femur of *Cynognathus*. The region of the clavicle and interclavicle of *Cynognathus* has been described by Broom (1909) and the missing upper part of the ilium was doubtless fundamentally similar to the same part in other therapsids, especially *Diademodon*. In the accompanying reconstruction (Plate XXXIX) the parts actually preserved are shaded, the missing parts are dotted. The most doubtful points of this reconstruction are the precise lengths of the limbs and the size of the feet. The drawings were made by Mrs. Elizabeth M. Fulda under the direction of the authors.

Seeley (1895, p. 97) gives the vertebral formula as C 6 (?), D 18, L 5, S 3, Cd ?, but a careful study of the casts indicates that it was very probably C 7, D 17, L 4, S 4, Cd ?. What Seeley calls the first cervical vertebra is evidently the axis with the attached pleurocentrum (odontoid) of the atlas, exactly as in *Dimetrodon*; the arch of the atlas and the pro-atlas are not preserved, but they have been described by Broom (1903) in another cynodont, *Gomphognathus kannemeyeri*. The atlanto-axis complex is essentially similar to that of monotremes and marsupials save for the retention of the pro-atlas. The first dorsal (Fig. 13, A) has the transverse process on a higher level than that of the last cervical as observed by Seeley. The ribs articulate with the transverse processes and between the vertebræ. The upper dorsal ribs were probably long and slender, as in *Microgomphodon eumerus*. The thirteenth to seventeenth ribs, inclusive, shorten up rapidly and project widely; near the proximal end they bear remarkable expansions, each of which overlaps the succeeding rib and is received into a concavity on its anterior border, so that there is, as it were, a set of secondary zygapophyses connecting these ribs. This remarkable specialization culminates in the lumbar series, in which the ribs lose the free portion of the shaft and end in widely flaring interlocking ends. This arrangement gives great strength to the lower dorsal and lumbar region; its possible adaptational significance is suggested below. There were very probably twenty-eight presacral vertebræ, the series being practically complete as to number. The same number of presacral vertebræ is recorded by Broom (1913) in the Dromasauria.

The vertebra which we identify as the first sacral (Fig. 13, A) is much like the lumbar, having on each side a distally expanded rib, which receives in its excavated anterior border the posterior blade of the rib in front of it;

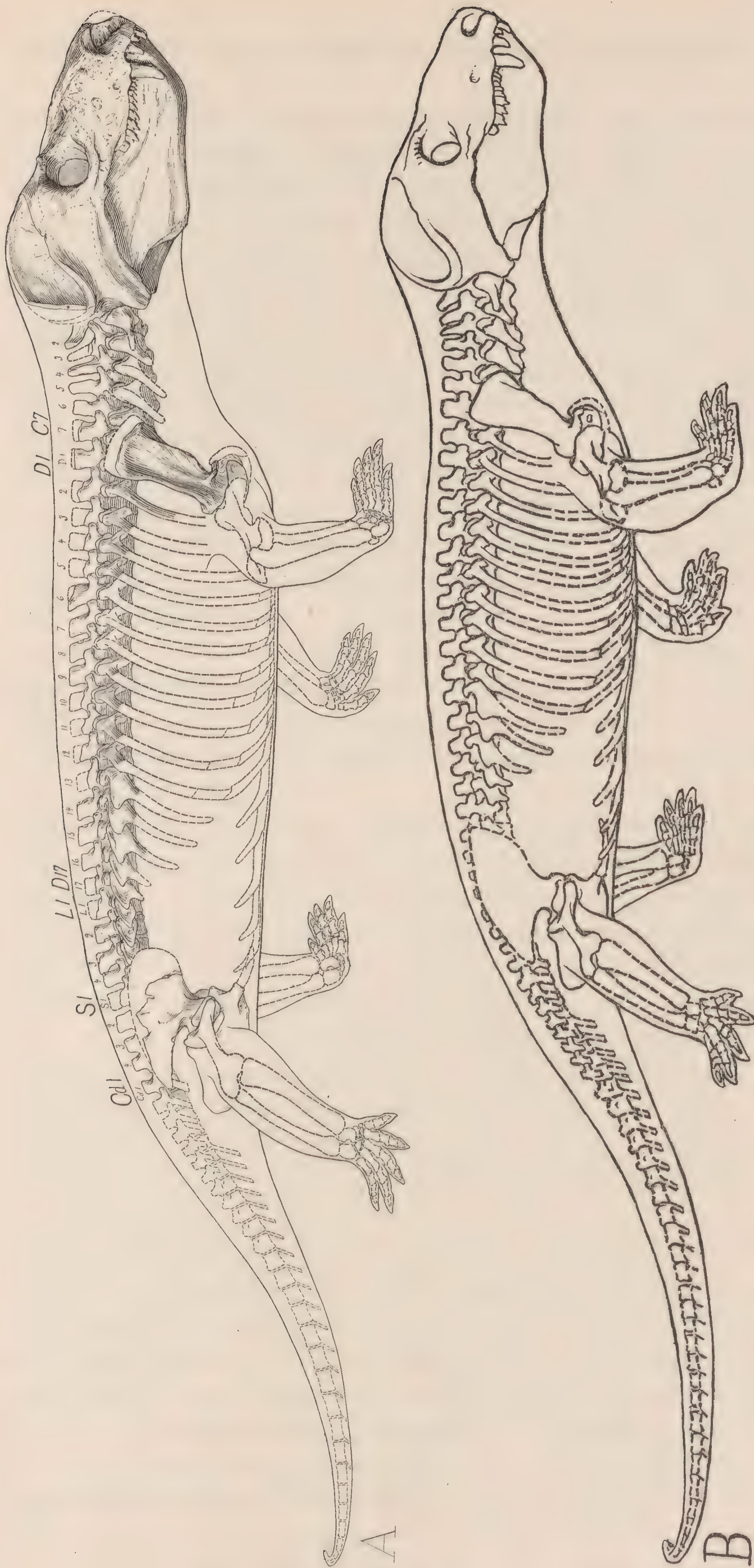


Fig. 13. Provisional reconstruction of *Cynognathus crateronotus* Seeley. About one-twelfth natural size.

A. First reconstruction. Fully shaded parts based on casts of the original skeleton. Dotted parts restored more or less conjecturally, chiefly from *Microgomphodon eumerus* Seeley, a nearly related animal. In this reconstruction the ilium is probably placed too low down on the sacral vertebrae.

B. Second reconstruction with corrected position of pelvis.

but the first sacral rib bears also on its posterior border a flattened expansion to which was probably attached the anterior extension of the ilium. Another reason for regarding this vertebra as the first functional sacral is that when the pelvis is placed below the true sacrals the anterior extension of the ilium comes opposite the first functional sacral rib as it does also in "*Microgomphodon*." (In our first restoration, Fig. 13, *A*, the ilium is probably placed too low with reference to the vertebræ). Thus the first functional sacral vertebra of *Cynognathus* may well represent a partly modified lumbar. The true sacrals are three smaller vertebræ which have their ribs connecting distally. According to Seeley the four caudal vertebræ following the last sacral are preserved and indicate that the tail was small.

A study of the scapulocoracoid in comparison with those of various reptiles and of monotremes (see pp. 510–512 above) indicates that the scapula was not turned backward over the ribs, as in typical mammals and certain reptiles, but that it was even inclined forward,¹ as in monotremes, and that the opposite scapulæ diverged widely.

The general form of the pectoral girdle and of the humerus approached the Monotreme type, with certain exceptions, so that probably the posture of the fore limbs was more like that of Monotremes than like that of primitive Placentals.

The scapula of the cynodonts (Pl. XL) is unique among reptiles in having the anterior border sharply everted, this foreshadowing the spina scapulæ of monotremes and other mammals, and in having an incipient prespinous fossa, beginning at the upper front corner of the scapula. The significance of this arrangement with reference to the muscular anatomy has been discussed above (p. 511). The reflected border runs down into a prominent acromial process forming the articular projection for the clavicle.

The humerus, which is restored from *Gomphognathus*, differs from the marsupial type especially in having the head flatter and much less differentiated from the shaft. It has a stout delto-pectoral crest (processus lateralis) and widely expanded distal end, as in other primitive reptiles and mammals.

The radius and ulna are partly known in *Microgomphodon*. The radius must have been markedly shorter than the tibia. The manus was probably short and spreading as in *Microgomphodon* and *Ælurosuchus*; not improbably there were ten elements in the carpus, including two free centralia. The fourth digit was the longest and digit III was nearly as long. The phalangea formula was very probably 2.3.3.3.3, as it is in the hind foot of "*Microgomphodon*."

In correlation with the wide expansion of the gluteal surface of the ilium,

¹ Watson comes to the same conclusion (Journal of Anatomy, Oct. 1917).

suggesting a corresponding development of the deep gluteal muscles; the femur has developed a very large great trochanter. The great size of the acetabulum is correlated with the widely oval head of the femur, which could be freely twisted in various directions. The projection of the iliac margin of the acetabulum and the emphasis of the cotyloid notch enable the head of the femur to be placed in such a way that the knees could be drawn forward more than in the primitive Permian reptiles. When resting or moving slowly, however, the knees were turned more outward. The pelvis below the acetabulum is more extended behind it than in front; this tendency is greatly emphasized in primitive mammals, birds and ornithischian dinosaurs, which all turn the femora forward, so that it again seems probable that, in running, *Cynognathus* turned the femora further forward than did the primitive Permian reptiles.

The lesser trochanter of the femur (Pl. XLVIII) is also approaching the mammalian position near the proximal end of the shaft, although more in the middle of the medial surface of the femur than in mammals. The tarsus is not well known even in "*Microgomphodon*." The foot of "*Microgomphodon*" is short and spreading.

The animal as a whole, which is restored in a slow-moving pose, has an extremely large head, short neck, short sprawling limbs, stout backbone, and fairly short tail. It parallels both the crocodilian and primitive mammalian types in its predatory habitus (including the carnivorous dentition, the secondary palate, and the marked differentiation of dorsal and lumbar regions). The sharp differentiation of the lumbar from the dorsal region probably indicates that the quadratus lumborum had begun to lose its metameric character — Gadow shows that it is the serial homologue of the intercostal muscles — and may indicate that this muscle was attached to the femur, as in alligators, while the pubi-ischio-femoralis internus may well have begun to differentiate into the iliopsoas and pectineus. The peculiar characters of the lower dorsal and lumbar ribs are possibly connected with the extremely large size and powerful musculature of the head which might require an equally strong development of the axial musculature, especially of the longus colli, recti capiti antici, and quadratus lumborum on the ventral side of the column, and of the complexus, spinalis, longissimus dorsi, and ilio-costalis on the dorsal side. The iliocostalis especially, was probably very large and to its great development the shortening of the lumbar ribs may perhaps be attributed. The sharp differentiation of the dorsal and lumbar region may also indicate that the muscular complex forming the diaphragm had already reached the lower dorsal region in its backward migration from the pericardium.¹ In any event, *Cynognathus* and *Micro-*

¹ Cf. Keith, A. 1913. *Human embryology and morphology*, pp. 337-340.

gomphodon retained true ribs, although of peculiar form, in the lumbar region, while in the mammals these have been replaced by outgrowths from the centra.

In general, the cynodonts foreshadowed the mammalian grade in a long list of characters of the skull and lower jaw and in the differentiation of the dorsal and lumbar regions, but, on the other hand, they retained the reptilian heritage in many characters of their limbs and girdles. They were doubtless normally sluggish animals, with rather small reptilian brains and imperfect heat-conserving and heat-producing adaptations, capable perhaps of stealthy pursuit and a sudden rush (straightening the hind limb somewhat in this movement), but not to be compared in speed or endurance with predatory cursorial mammals.

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PART VI.—SECOND NOTE ON THE EVOLUTION OF THE CORACOID ELEMENTS IN REPTILES AND MAMMALS

BY W. K. GREGORY

The present note is a sequel to the brief discussion of the long-standing coracoid problem published in 1915.¹ At that time the facts recorded by Parker, Howes, Lydekker, Broom, Williston, and others, led the writer to the conclusion that three distinct parts of the coracoid complex are involved in the problem of the homologies of the "coracoids" of reptiles and mammals and not two, as assumed by previous investigators:

(a) the epicoracoid, of *Sphenodon*, lizards, and monotremes, a sheet of bone lying immediately above the clavicles and never reaching the glenoid surface;

(b) the true coracoid, or so-called precoracoid, lying behind the clavicles, originally pierced by the coracoid foramen, forming at least the front part of the glenoid, often articulating with the sternum; and

(c) the metacoracoid, of Permian reptiles, originally forming the back part of the glenoid region, lost in later reptiles (Williston) and in mammals, except when preserved as a vestigial element (Howes).

This view was in opposition to that of Broom (1912) who held that there were only two elements involved, of which the posterior element (metacoracoid) gave rise to the coracoid of mammals, while the anterior one (precoracoid) gave rise to that of birds and of those reptiles which have a single coracoid.² Dr. Broom homologized the epicoracoid and coracoid elements of monotremes with the "precoracoid" and "metacoracoid," respectively, of South African mammal-like reptiles, a comparison which has at first sight a great appearance of truth for it is difficult to realize that the monotremes have lost the metacoracoid and, as will be shown below, that the therapsids and other Permian reptiles probably had a thin epicoracoid in front of the precoracoid. We must also assume, if the coracoid of monotremes represents the "precoracoid" of therapsids, that the precoracoid foramen and its nerve, which are such constant features in reptiles, have been lost in mammals. But, as this foramen is absent in the coracoid of many birds, which is plainly homologous with the "precoracoid," its absence in monotremes does not constitute a serious objection to the supposed

¹ Ann. N. Y. Acad. Sci., XXVI, pp. 369-375.

² Watson also, in a paper which was received too late for extended notice here (Journal of Anatomy, October, 1917), holds that the metacoracoid of Permian reptiles gave rise to the true coracoid of mammals.

homology of the monotreme coracoid with the precoracoid of Permian reptiles.

Professor Williston's discoveries and observations on American Permian reptiles have afforded very strong evidence amounting almost to a demonstration that the "single coracoid" of lizards, *Sphenodon*, and other typical reptiles represents not a fusion of the pre- and metacoracoids but the precoracoid alone.

The studies of the junior author have revealed the fact (hitherto scattered in the literature of myology) that the single coracoid of *Sphenodon* (Pl. XLIX), homologous with the precoracoid and pierced by the precoracoid foramen, gives origin on its ventral surface to a group of muscles comprising the biceps and the three branches of the coracobrachialis, which group appears to be precisely homologous with a similar group of muscles carried by the ventral surface of the coracoid of monotremes. The dorsal surface of the coracoid in *Sphenodon* gives origin to the whole of the subcoracohumeralis. In monotremes an homologous muscle (subcoracoideus) likewise arises in part from the dorsal surface of the coracoid but, as it is very large, it also extends over the dorsal surface of the epicoracoid. The arrangement of the muscles, therefore, appears to confirm the homology of the coracoid (= precoracoid) of *Sphenodon* with the coracoid of monotremes.¹

Comparison of the monotreme shoulder-girdle with that of the alligator (Pl. L) adds further evidence in the same direction; for not only is the single perforated coracoid of the alligator essentially like the true coracoid of *Ornithorhynchus* in form and position but it also gives origin to the biceps, coracobrachialis, and supracoracoid muscles, the latter likewise extending on to the epicoracoid membrane.

The epicoracoid of *Sphenodon* is widely excluded from the glenoid, exactly like the epicoracoid of monotremes; it also has identical relations with the clavicle and interclavicle. The epicoracoid of both *Sphenodon* and monotremes carries the anterior part of the supracoracoid muscle, or epicoracohumeralis, on its ventral surface.

The whole complex of relations of the epicoracoid and coracoid of monotremes to each other and to the scapula, clavicle, and interclavicle is practically identical with the relations of the same set of elements in lizards and *Sphenodon* as shown in the accompanying figures. But, if the epicoracoid of monotremes be not homologous with that of *Sphenodon* and lizards, we have to imagine a bewildering set of substitutions, not only among these elements but also of the muscles they carry, for which we have but little

¹ It is only fair to state, however, that Watson (*op. cit.*) cites the position of these muscles in *Sphenodon* and the Monotremes in support of the opposite conclusion.

evidence. The epicoracoid, which must have bordered the precoracoid of the ancestral Permian types as a thin unossified sheet, would have to disappear in the mammalian line and the precoracoid would have to take its place, while at the same time the muscles would have to shift in such a way that the biceps-coracobrachialis group would finally lodge upon the metacoracoid in mammals and upon the precoracoid in reptiles. Such assumptions seem to be more difficult to accept without direct evidence than the inference that the ancestors of the mammals, as well as other progressive reptiles and birds, tended to lose the metacoracoid. And, when we realize that in very many parts of their anatomy the monotremes have advanced far beyond the mammal-like reptiles and that even in their coracoids they bear only a general resemblance to them, it becomes less incredible that they should have progressed also in the matter of losing the metacoracoid, even while retaining the ancient contact of the precoracoid (= true coracoid) with the sternum.

That the Permian therapsid reptiles did have a membranous epicoracoid in front of the "precoracoid" is indicated by the fact that in assembling the parts of the shoulder-girdle of *Moschops* it was found that there was a space between the clavicles, interclavicles, and precoracoids which must have been filled by the epicoracoids, as in *Sphenodon* and lizards. In *Eryops* also the anterior edges of the coracoids clearly indicate the presence of a membranous epicoracoid.

It is probable that in the therapsid-mammal group the metacoracoid persisted longer than in some of the more typical reptilian phyla. In the Triassic cynodont *Cynognathus* (Fig. 14) it is still very well developed and, owing to the total lack of mammalian skeletons from the Jurassic and Cretaceous, its reduction and disappearance during those periods will perhaps never receive direct palæontological proof. The metacoracoid was perhaps only one of many elements of the endoskeleton of primitive reptiles which, as it were, lacked vitality and were gradually eliminated in all later phyla.

The selection of the precoracoid rather than the metacoracoid as the survivor of the two original elements is possibly connected with the fact that in all progressive phyla there was a tendency to draw the elbows in toward the body, which caused the chief pressure from the head of the humerus to be exerted on the anterior, or precoracoid, part of the glenoid fossa. In this way the articular surface was gradually shifted forward. Meanwhile the head of the humerus and the glenoid cavity were enlarging and tending to crowd the metacoracoid away from its contact with the scapula, so that even in *Moschops* the connection between the metacoracoid and the scapula was small and weak (Fig. 15). The true coracoid, on the other hand, was broadly braced by the scapula and by the epicoracoid, so

that when the connection with the sternum was broken, through the reflection of the scapula, the coracoid adhered to the scapula.

A fourth element in the coracoid complex which has given rise to much confusion is the "subcoracoid center" of placental mammals, which Howes, Lydekker, and others regarded as the last vestige of the metacoracoid. We have verified the occurrence of this element, which finally fuses with the scapula, in many orders of placental mammals but we were unable to find it

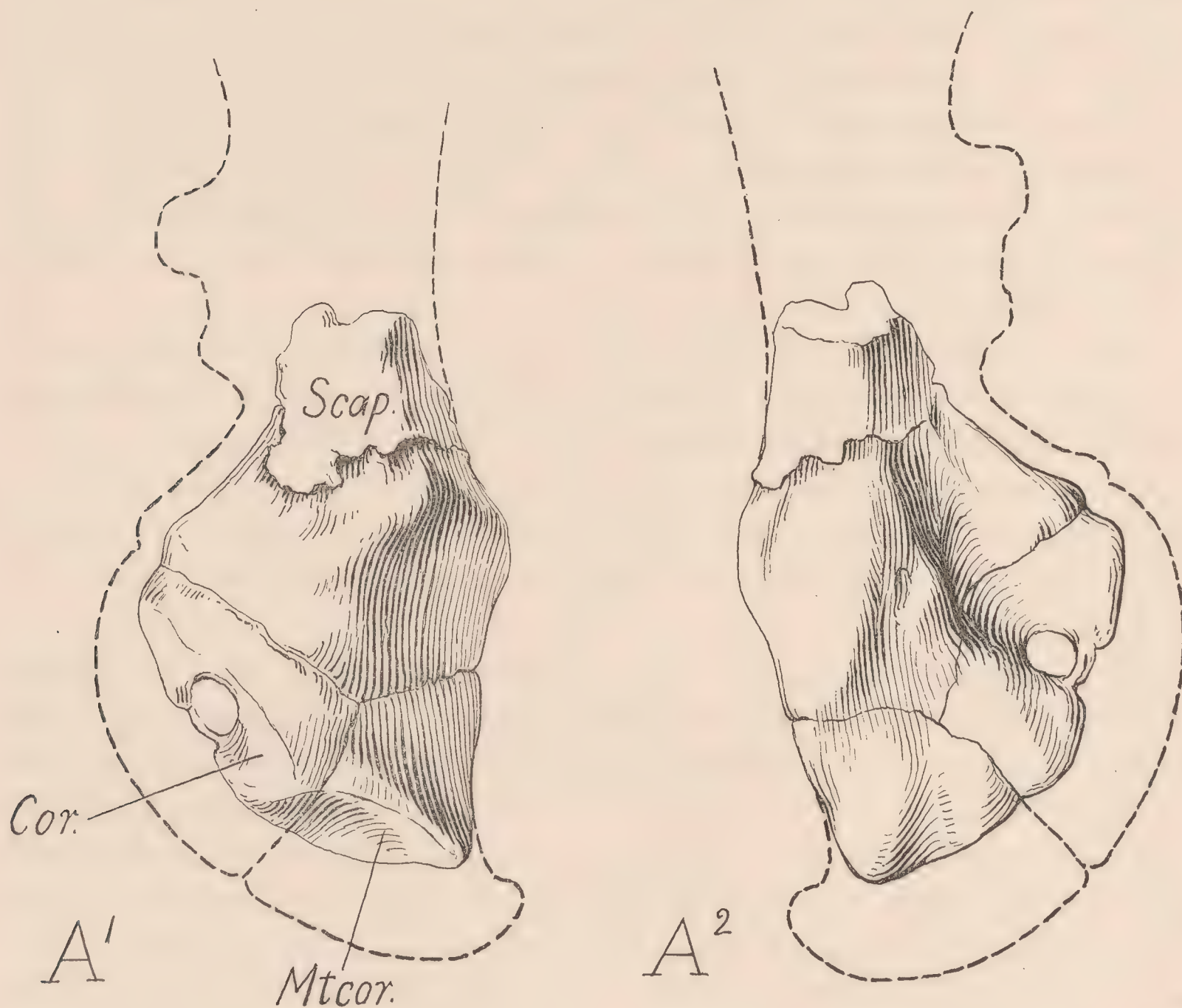


Fig. 14. Relations of the coracoid, metacoracoid and scapula in *Cynognathus* sp., Broom collection, A. M. N. H. $\times \frac{3}{2}$.

The surface of the bone is largely missing, but the interior is represented by a natural cast of the glenoid region, which clearly shows the sutural relations of the three elements. The coracoid is perforated by the supracoracoid foramen. The metacoracoid has a wide contact with the scapula.

either in the marsupials or the monotremes, although in the two last named groups we had only one or two young specimens. In placental mammals it always forms the front part of the glenoid fossa immediately behind the coracoid; it is located at the anterior end of the glenoid ligament where the

latter is continuous with the long tendon of the biceps. This muscle in placentals passes through the capsule of the shoulder-girdle but in marsupials and monotremes, which apparently lack the subcoracoid, the biceps does not pass through the capsule but arises from the overlying coracoid (Carlson, Leche). As the intrascapular position of part of the biceps is undoubtedly a neomorph in the placentals, we suspect that the appearance of a subcoracoid center of ossification is also a neomorph, like the ossific centers



Fig. 15. Relations of the scapula, coracoid and metacoracoid in *Moschops capensis* Broom. Based on specimens in the Broom collection, A. M. N. H. The metacoracoid has a weak contact with the scapula.

in the acromian and the center at the lower tip of the coracoid. These and similar accessory centers appear to be associated with the attachments of muscles or ligaments.

Ameghino (1908), in a paper which the writer has only recently taken

into consideration, has given many carefully drawn figures of the coracoid region in various edentates. His identification of the coracoid elements in *Dicynodon* (*op. cit.*, p. 65), in the opinion of the writer, is correct, but he agrees with Howes in regarding the "subcoracoid" of mammals as the homologue of the reptilian metacoracoid, a conclusion which the writer has felt obliged to abandon. His identification of the main coracoid of Crocodilia, lizards, and ichthyosaurs as "metacoracoid" is not in accordance with the cogent evidence since secured by Professor Williston, which tends to show that the single coracoid of these reptiles represents the anterior, or perforated

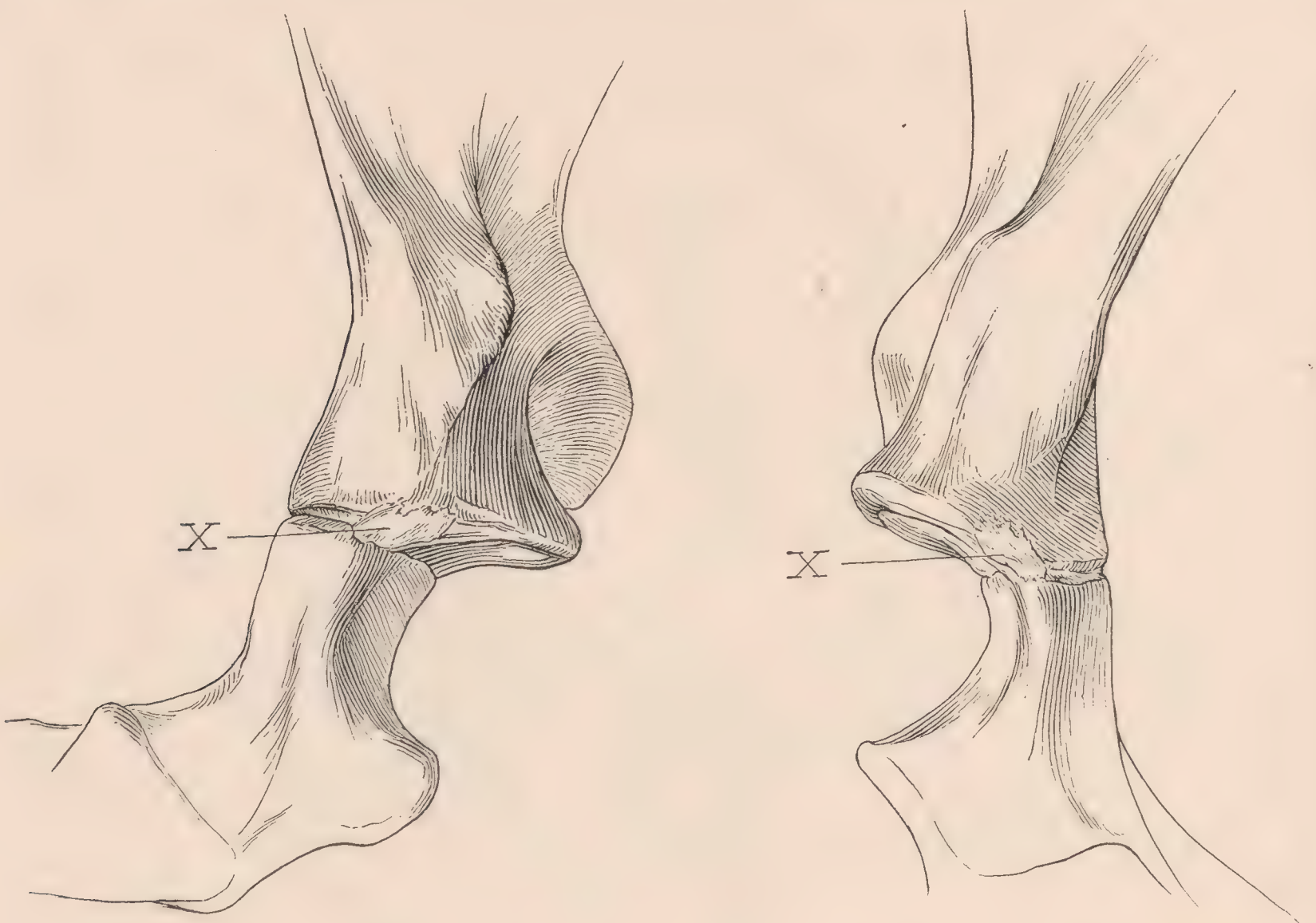


Fig. 16. Posterior aspect of the right and of the left glenoid region of an immature *Echidna aculeata*. Considerably enlarged.

A small epiphyseal (?) ossicle (X) is present on both sides at the posterior margin of the glenoid fossa and at the sutural junction of the scapula and coracoid. While in the right position for a vestigial metacoracoid, its true meaning and homology are very doubtful.

coracoid. In his figure (p. 76) of an abnormal pectoral girdle of *Echidna* the "precoracoid" is precisely in the position of the glenoid portion of the precoracoid of therapsid reptiles. If this be confirmed as a fact it would tend to some extent to support his conclusion.

In conclusion, the interpretation of the coracoid complex herein provisionally adopted may be summarized thus:

	PLACENTALS	MARSUPIALS	MONOTREMES	PRIM. PERMIAN REPTILES	MODERNIZED REPTILES	BIRDS
EPICORACOID	Absent in adults	Vestigial in em- bryos	Well developed	Probably present as a thin sheet of bone	Present	?“Precoracoid” of <i>Ratites</i>
CORACOID	Coracoid process	Coracoid process	Coracoid	“Precoracoid”	Coracoid	Coracoid
METACORACOID	Absent	Absent	Absent	Well developed	Absent	Absent
SUBCORACOID	Present (Neomorph)	Not developed	Not developed	Not developed	Not developed	Not developed

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SUMMARY AND CONCLUSIONS

BY W. K. GREGORY

(1) The homologies of the limb muscles in reptiles and mammals as worked out by Fürbringer and Gadow from the innervation and from the origin, insertion, and relations of the muscles are, with few exceptions, adopted provisionally as the basis of the present work.

(2) The supposed homologies of the muscles of the pectoral region of reptiles and mammals are summarized on pages 477-479.

(3) The supposed homologies of the muscles of the pelvic region of reptiles, birds, and mammals are summarized on pages 504-505.

(4) The provisionally adopted homologies of the tail muscles of reptiles and mammals are summarized on pages 506-507.

(5) The general locations of the principal muscles of the pectoral and pelvic regions of *Cynognathus* are inferred after a critical comparison of the corresponding skeletal parts of *Cynognathus* and related forms with those of recent reptiles and mammals, in which the skeletal characters are correlated with known arrangements of the muscles. *Cynognathus* is a favorable subject for this kind of reconstruction because its girdles and limbs, while fundamentally reptilian, exhibit certain well marked modifications in the direction of the mammalian, and especially of the monotreme, type; so that it is fair to assume that the musculature of these parts was equally progressive toward the mammalian type. The inferred positions of the muscles of *Cynognathus* are given on pages 451-502 and in plates XXXIX-XLII, XLIV, XLV, while some of the reasons for these conclusions are discussed on pages 508-514.

(6) The chief contrasts in skeletal characters and musculature of the girdles and limbs between the primitive reptile *Sphenodon* and a highly specialized bipedal mammal (man) are correlated with equal differences in posture and it is pointed out that these wide contrasts are, to a certain extent, mediated by the conditions observable in the monotremes (pp. 509, 513).

(7) As bearing especially on the musculature of *Cynognathus*, it is noted (p. 510) that this animal shares with *Sphenodon* the primitive reptilian character of the upper end of the scapula, while it resembles monotremes in the sharp reflection of the anterior border to form the spina scapulæ, which ends below in the acromial process for the clavicle. It is, therefore, inferred (p. 511) that the everted surface of the scapula was occupied on the anterior side chiefly by enlarged omotrachelian and levator scapulæ muscles, as in

monotremes, and that the postspinous fossa was already occupied, as in monotremes, by the infraspinatus muscle (which is supposed to be a derivative of the reptilian scapulo-humeralis posterior). The coracoid region is, on the whole, nearer to the monotreme type in general form, but very probably differed in the lack or feeble development of an epicoracoid fenestra, from which it is inferred that the supraspinatus muscle was still a part of the supracoracoideus and had not yet migrated dorsally or driven out the omotrachelian from the prespinous surface.

(8) It is shown (pp. 512, 513) how the wide contrasts in the pelvic region between *Sphenodon*, a primitive crawling reptile, and *Homo*, an advanced bipedal mammal, are correlated with corresponding differences in the arrangement and form of the muscles and with equal differences in the normal posture and function of the limbs. Among other differences it is noted that in *Homo* the gluteal area on the ilium is greatly expanded and the insertions of the primitive tail muscles greatly reduced or absent; that the iliacus area on the front inner side of the ilium is also widely expanded; that a certain group of muscles, including psoas major, iliacus, and pectineus, has very probably been derived from the pubi-ischio-femoralis internus of reptiles, as held by Gadow and others (pp. 486, 504).

(9) It is noted (p. 513) that, in the form and musculature of the pelvis, the monotremes again mediate the difference between *Sphenodon* and *Homo* and that, as regards the skeletal parts, *Cynognathus* in turn divides the difference between *Sphenodon* and the monotremes. In *Cynognathus* the forward expansion of the gluteal area of the ilium and the robust development of this group of muscles are correlated with the development of a large external trochanter on the femur. In the construction of the pubi-ischiadic plate *Cynognathus* is much closer to monotremes than to either *Sphenodon* or *Alligator* and it is accordingly inferred (Pl. XLV) that the arrangement of the obturator externus, adductors, gracilis, obturator internus, quadratus femoris, gemelli, biceps, semitendinosus, and semimembranosus was fundamentally as in monotremes, although doubtless more primitive in some respects.

(10) The probable homologies of the pelvic muscles in reptiles and birds, as worked out chiefly by Gadow, are summarized in the table on pages 504, 505, in which also comparisons with monotreme and placental mammals are given.

(11) After a comparative study of the pelvis of *Struthio*, *Alligator*, *Cynognathus* and *Ornithorhynchus*, drawings are given (Plate XLVI) showing the location of the muscle areas in these animals and the inferred location of the muscle areas in a saurischian dinosaur *Ornitholestes hermanni*. It is noted (p. 515) that, in spite of the general resemblance of the ilium of thero-

podous dinosaurs to that of birds, their pelvis is of reptilian type, with the pubis directed downward and forward, instead of downward and backward, and, hence, that it is reasonable to infer that the lower pelvic muscles were still in their primitive reptilian positions, rather than in the backwardly displaced positions seen in ornithischian dinosaurs and birds. (Some further consequences of these facts will be discussed in a later number of these studies.)

(12) In a review of the origin and evolution of certain locomotor adaptations in the pectoral and pelvic regions it is noted that in the earlier stages of evolution the movements of the paired limbs were closely correlated with, and at first subordinate to, the undulatory movements of the axial skeleton and musculature (p. 517), while in the highest stages the limb movements and musculature become widely differentiated from those of the axial skeleton. At the same time the originally metameric character of the limb muscles is progressively disguised.

(13) In primitive tetrapods the pelvis is located at the intersection of three main series of muscles (p. 518): first, those running from the pelvis and femur forward; second, those running from the pelvis and femur backward; third, those running transversely from the pelvis to the limb, both above and below the femur.

(14) The deep gluteal muscles are specialized anterior portions of the lateral tail muscles, while the superficial gluteus and agitator caudæ have probably been derived from the obliquus abdominis externus, as suggested by Gadow (p. 518).

(15) In the most primitive reptiles the deep gluteal muscles and the gluteal surface of the ilium are but little expanded. In large, heavy, and highly specialized reptiles, on the contrary, the gluteal muscles and gluteal surface of the ilium become greatly expanded (p. 519).

(16) While the muscles of one side are moving the free limb forward, the corresponding muscles of the opposite side, with the assistance of the back and tail muscles, are holding up the body on the limb that is on the ground and preventing the body from falling or sagging to one side. Thus we have adaptational reasons, on the one hand, for the expansion of the ilium and the extension of the sacrum in animals that hold the body well raised from the ground and, on the other hand, for the decrease in size and retrogression of the sacrum in fully aquatic types, which are buoyed up by the water (pp 519, 520).

(17) In forward locomotion, both on the ground and in swimming, the pelvis as a whole is turned alternately from side to side and rocked in a transverse plane. An attempt is made (p. 520) to describe the movements of the pelvis in connection with the action of the pelvic and caudal muscles.

(18) In primitive reptiles the ilium lies directly above the acetabulum, the pubis below and in front of it, and the ischium below and behind it. The femur in these types is ordinarily directed outward and the knees are permanently flexed. In mammals, on the other hand, the ilium is extended in front of the acetabulum, while the pubi-ischiadic rami lie chiefly behind it. The femur can be directed sharply forward and the knees can be widely extended. As a result of these changes, the obturators and adductors tend to pull the femur backward as well as inward, while the deep glutei also contribute a powerful anteroposterior component (pp. 521-523).

(19) A like purpose was probably served in birds and ornithischian dinosaurs by the anteroposterior extension of the ilium and of the anterior process of the pubis, as well as by the posterior extension of the pubis and ischium.

(20) In birds the "pectineal" or prepubic process serves for the attachment of one branch of the ambiens (rectus femoris). In ornithischian dinosaurs the greatly enlarged prepubic process may have served for the attachment not only of the ambiens and pubi-ischio-femoralis externus on the outer side, but also of the pubi-ischio-femoralis internus on the inner side (p. 521).

(21) In primitive reptiles the whole proximal end of the femur, forming a widely oval flattened head, was thrust into the wide, more or less three-sided acetabulum. In primitive mammals, on the other hand, the proximal end of the femur is differentiated into a spherical head, a distinct neck, and a projecting great trochanter for the attachment of the deep gluteal muscles. These and other differences were correlated with the contrasting posture of the limbs during locomotion in reptiles and mammals (pp. 524, 525).

(22) The fore limb of primitive vertebrates presents many analogies in structure and function with the hind limbs (p. 525). Just as in the hind limbs there is a set of muscles running from the vertical blade of the girdle posteriorly, a second set running from the girdle anteriorly and a third set running from the girdle transversely both above and below the fulcrum.

(23) The origin and subsequent disappearance of the cleithrum is referred to (p. 526), as well as the freeing of the pectoral girdle from its former attachment to the occiput.

(24) Primitive tetrapods still retain much of the piscine mode of undulation of the body in anteroposterior progression. This is accomplished partly through the axial musculature, partly through the action of the longitudinal muscles running along the side of the neck to the scapula and from the scapula back to the ribs. The lateral movements of the pectoral arch and sternum are described (pp. 526, 527), as well as the correlated movements of the fore and hind limbs in quadrupedal reptiles (p. 527).

(25) The various trochanters of the femur in reptiles, birds, and mammals are reviewed, and the relations of the trochanters to the muscles are considered (pp. 328-335). It is concluded that the lesser trochanter of mammals and the fourth trochanter of birds and dinosaurs are divergent derivatives of the internal trochanteric, or adductor, crest of primitive reptiles. The lesser trochanter of mammals, representing the upper or proximal part of the primitive trochanteric crest, points forward and is associated with the pubi-ischiofemoralis internus (= iliopsoas + pectineus). The fourth trochanter, derived from the more distal part of the primitive trochanteric crest, points backward and is associated especially with the adductors and caudifemoralis. The third trochanter is a neomorph in placental mammals.

(26) A reconstruction of the skeleton of *Cynognathus crateronotus* Seeley (pp. 538-545) is attempted after repeated studies of the available material, and in the light of the facts and principles above noted. A revised description of the more salient skeletal characters is given. It is concluded that the cynodonts foreshadowed the mammalian grade in many well-known characters of the brain-case and jaws, in the differentiation of the dorsal and lumbar regions, in the eversion of the anterior border of the scapula to form the spina scapulæ, in the forward extension of the ilium, and in the characters of the manus and pes. On the other hand, they were by definition reptiles, since the quadrate still functioned as such and the squamosodentary joint was not yet established. They also retained the reptilian heritage in many other characters, e. g., the presence of true ribs in the lumbar region, the presence of a metacoracoid, the lack of a well developed prespinous fossa in the scapula, the large size of the acetabulum, and the width and flatness of the head of the femur. They were doubtless normally sluggish animals, with small reptilian brains and imperfect heat-conserving and heat-producing adaptations, capable perhaps of stealthy approach and a sudden rush (straightening the hind limb somewhat in this movement), but not to be compared in speed or endurance with predatory cursorial mammals.

(27) In the "Second Note on the Evolution of the Coracoid Elements in Reptiles and Mammals" (pp. 545-552) it is maintained that three distinct parts of the coracoid region are involved in the problem of the homologies of the "coracoids" of reptiles and mammals: viz, the epicoracoid, the true coracoid (precoracoid), and the metacoracoid, as defined above (p. 545). The arrangement of the coracobrachialis and biceps muscles in reptiles and mammals are cited in support of this view and it is also claimed (p. 546) that the Permian reptiles probably had a membranous epicoracoid in front of their precoracoids (or true coracoids). It is suggested that the metacoracoid

was only one of the many elements of the endoskeleton of primitive reptiles which, as it were, lacked vitality and were gradually eliminated in all later phyla and that mammals in this respect followed the same line of evolution as did all other tetrapods which have but a single coracoid. It is held (p. 548) that the "subcoracoid center" has nothing to do with the ancient meta-coracoid elements but is a neomorph in the placental mammals, associated with the intrascapular attachment of the tendon of the long head of the biceps. A summary of the various coracoid elements of reptiles, birds and mammals is given on p. 551.

EXPLANATION OF PLATES

PLATE XXXIX

Diagrams showing the probable position of the chief muscles of the pectoral region in *Cynognathus*.

A¹ — Superficial muscles after the removal of the skin and of the sphincter colli.

A² — Deeper muscles after the removal of the sphincter colli, trapezius and latissimus dorsi.

PLATE XL

Scapulocoraco-metacoracoid of *Cynognathus crateronotus* (cast of original specimen) with the probable muscle areas.

A¹— Medial aspect. A²— Lateral aspect.

This region is on the whole much more like that of *Ornithorhynchus* than like those of either *Sphenodon* or *Alligator*. The omotrachelian (= levator scapulæ superficialis superior of *Sphenodon*) had a wide area on the cranio-medial surface of the reflected anterior border (= spina scapulæ). The post-spinous fossa was probably occupied by a large infraspinatus (= scapulohumeralis posterior?). This muscle, however, according to Fürbringer, is not the homologue of the similarly placed scapulohumeralis posterior of *Sphenodon*, but has been derived from the supracoideus (epicoracohumeralis), a part of which is supposed to have migrated dorsally and crowded out the scapulohumeralis posterior. In that case the latter may possibly be represented by the infraspinatus secundus of ungulates. The teres minor may have been inserted on a small rugosity above the glenoid fossa; it may represent part of a reduced dorsalis scapulæ, the spino-deltoid representing the other part.

PLATE XLI

Inferred general position and relations of the chief muscles of the shoulder region in *Cynognathus* (A) as compared with the known facts in *Ornithorhynchus* (B). Right side, lateral aspect.

PLATE XLII

Inferred general position and relations of the muscles of the pectoral girdle in *Cynognathus* (A) as compared with the known facts in *Ornithorhynchus* (B). Front view.

In *Cynognathus* the right clavicle is omitted in order to expose the muscles beneath and behind it. The width across the opposite acromia is conjectural. The suprascapulæ as restored are probably much too small.

PLATE XLIII

Musculature of the pelvic limbs of recent reptiles. After Gadow.

A.—*Hydrosaurus* (*Varanus*) *marmoratus*. Medio-ventral aspect of the right hind limb with oblique medial view of the right half of the pelvis and associated muscles. After Gadow, 1882, Fig. 36.

S, Il. sacro-iliac articulation (disconnected).

a, b, c, plexus cruralis (first, second, third presacral nerves).

Of these, c gives a branch to the ambiens and another to the iliofemoralis; b contributes largely to the obturator nerve, which traverses the obturator foramen in the pubis. The sacral nerve (NS) is the nerve that issues between the two sacral vertebræ; its plexus (Pl. ischiadicus s. sacralis) sends branches to the caudi-iliofemoralis, the caudifemoralis and the pubi-ischio-tibialis and the femorotibialis (Gadow, 1882, Taf. XVII, Fig. 16).

The plexus pudendus (α) sends branches to the cloacal and perineal region, and to the caudi-femoralis.

<i>rect.</i>	rectus abdominis
<i>p. is. f. int.</i>	pubi-ischiofemoralis internus, arising on inner surface of pubis and ischium
<i>p. is. f. ext.</i>	pubi-ischiofemoralis externus, arising on outer surface of pubis and ischium and seen through the thyroid fenestra
<i>e. il. tb.</i>	extensor iliotibialis
<i>amb.</i>	ambiens
<i>fm. tb.</i>	femorotibialis
<i>pb. tb.</i>	pubitibialis
<i>pb. is. tb.</i>	pubi-ischiotibialis
<i>tb. ant.</i>	tibialis anticus
<i>cap. int.</i>	} gastrocnemius
<i>cap. ext. gastr.</i>	
<i>fl. t. int.</i>	flexor tibialis internus
<i>pb. is. fm. post.</i>	pubi-ischiofemoralis posterior
<i>is. cd.</i>	ischiocaudalis
<i>cd. fm.</i>	caudifemoralis

B.—*Hatteria* (*Sphenodon*) *punctata*. Right pelvic region, ventral view. After Gadow, 1882, Fig. 40. Portions of the rectus abdominis ventralis and of the pubi-ischiotibialis have been cut away to show the underlying muscles.

<i>rect.</i>	rectus abdominis (ventralis)
<i>rect. int.</i>	rectus internus abdominis
<i>Sy. p., Sy. is.</i>	symphysis pubis, symphysis ischii
<i>p. is. f. ext.</i>	pubi-ischiofemoralis externus
<i>os. c.</i>	os cloacæ
<i>is. cd.</i>	ischiocaudalis
<i>p. is. f. int.</i>	pubi-ischiofemoralis internus, part III (inserted on the anterior and partly on the inner surface of the femur)
<i>cd. fm.</i>	tendon of the caudifemoralis near its insertion distal to the external trochanter
<i>is. fm.</i>	ischiofemoralis
<i>fm. tb.</i>	femorotibialis

<i>pb. tb.</i>	pubitibialis
<i>amb.</i>	ambiens
<i>fl. tb. int.</i>	flexor tibialis internus
<i>pb. is. tb.</i>	pubi-ischiotibialis
<i>fl. t. ext.</i>	flexor tibialis externus
<i>il. f.</i>	iliofemoralis

C.—*Alligator mississippiensis*. Pelvic region, lateral aspect. After Gadow, 1882, Fig. 34.

<i>quadr. lb.</i>	quadratus lumborum, extending downward and backward towards its insertion on the femur
<i>obl. ext.</i>	obliquus externus abdominis
<i>amb.</i>	ambiens, piercing quadratus lumborum on its way toward insertion on the ilium
<i>e. il. tb. 1, e. il. t. 2</i>	first and second branch of the extensor iliotibialis

The nerves in this region come from the crural plexus.

<i>il. fm.</i>	iliofemoralis
<i>f. t.</i>	femorotibialis

The long nerve behind the femorotibialis is the nervus obturatorius.

<i>il. fb. 1, il. fib. 2</i>	iliofibularis, parts 1, 2
<i>f. t. ext.</i>	flexor tibialis externus
<i>f. t. int.</i>	flexor tibialis internus
<i>cd. il. fm.</i>	caudi-iliofemoralis
<i>cd. fm.</i>	caudifemoralis
<i>y</i>	tendinous branch of the caudifemoralis running to the caput fibulæ
<i>is. cd.</i>	ischiocaudalis
<i>N. cut.</i>	cutaneous branch from the sacral plexus

D.—*Hatteria (Sphenodon) punctata*. Right side, latero-dorsal aspect, after the removal of sections of the extensor iliotibialis, iliofibularis and iliocaudalis. After Fürbringer, 1882, Fig. 39.

<i>os.</i>	ilium
<i>il. fib.</i>	iliofibularis
<i>cd. il. f.</i>	caudi-iliofemoralis
	long tendon of caudi-iliofemoralis
<i>il. cd.</i>	iliocaudalis
<i>pr. tr.</i>	transverse processes, above which run the segmental dorsal muscle of the tail (M. caudæ dorsalis)
<i>cd. fm.</i>	caudifemoralis
<i>rect.</i>	rectus abdominis
<i>p. l. p.</i>	processus lateralis pubis
<i>e. il. t.</i>	extensor iliotibialis (connecting anteromedially with the thin tendon of the pubi-ischiofemoralis internus, part I)
<i>p. is. f. int. (III)</i>	pubi-ischiofemoralis, part III
<i>amb.</i>	ambiens
<i>il. fm.</i>	iliofemoralis
<i>fm. tb.</i>	femorotibialis
<i>is. t.</i>	ischiotibialis
<i>fl. tb.</i>	flexor tibialis (internal head)

E.—*Alligator mississippiensis*. Sagittal section of the pelvic region, medial aspect. After Gadow, 1882, Fig. 33.

<i>obliq.</i>	obliquus abdominis
<i>transv.</i>	transversus abdominis
<i>quadr. lumb.</i>	quadratus lumborum

The segmental nerves in this region form part of the plexus cruralis.

p. is. f. int. (I) pubi-ischiofemoralis internus, part I.

This part is pierced by the obturator nerve which is seen passing between the os pubis (*o. p.*) and the ischium (*Sy. i.*)

p. is. f. ext. pubi-ischiofemoralis externus

is. f. ischiofemoralis

p. is. f. int. (III) pubi-ischiofemoralis internus, part III, arising from the inner surface of the 24th, 25th and 26th vertebræ. Medial to this muscle is the plexus sacralis.

p. is. f. post. pubi-ischiofemoralis posticus

cd. il. fm. caudi-iliofemoralis

cd. fm. caudifemoralis, attached to the chevrons

is. cd. ischiocaudalis

PLATE XLIV

First trial diagram showing the inferred general location and relations of the principal muscles of the pelvic region in *Cynognathus*.

<i>sacro. spin.</i>	sacrospinalis
<i>quadr. lumb.</i>	quadratus lumborum. This muscle may have extended further ventrally and might have even been attached to the upper part of the femur as in the alligator
<i>obl. abd. ext.</i>	obliquus abdominis externus, inserted partly on the epipubic bones
<i>sart.</i>	sartorius, derived from anterior part of extensor iliotibialis, part X
<i>glut. max.</i>	ectogluteus tensor fasciæ, derived from posterior part of extensor iliotibialis
<i>pub. isch. fem. int.</i>	pubi-ischiofemoralis internus (= psoas major + iliacus + pectineus). Probably much larger than as shown here
<i>ambiens</i>	ambiens (rectus femoris). The rest of the quadriceps (femorotibialis) is not shown
<i>caud. il. fem.</i>	caudi-iliofemoralis (giving rise to deep glutei, pyriformis, etc.)
<i>caud. fem.</i>	caudifemoralis, inserted on postero-medial surface of femur
<i>caud. dors.</i>	M. caudæ dorsalis (extensors)
<i>ilio. caud.</i>	iliocaudalis (abductor caudæ dorsalis)
<i>isch. caud.</i>	ischiocaudalis (abductor caudæ ventralis, coccygeus)
<i>add. brev.</i>	adductor brevis (= part of pubi-ischio-femoralis)
<i>add. long.</i>	adductor longus (= part of pubi-ischio-femoralis)
<i>gracilis</i>	(?derived from pubi-ischiotibialis)
<i>semimemb.</i>	semimembranosus (?derived from ischiotibialis)
<i>biceps</i>	?derived from iliofibularis

PLATE XLV

General location of the muscle areas of the pelvis of *Sphenodon* (*A*¹, *A*²), *Ornithorhynchus* (*B*) and *Cynognathus* (*C*). (Compare Plate XLVI).

*A*¹—*Sphenodon*, right half of pelvis, medial aspect. Muscle areas according to Osawa (1898) and Gadow (1882).

*A*²—The same, lateral aspect. Muscle areas according to Osawa and Gadow.

<i>S₁S₂</i>	articular surfaces for sacral vertebræ
<i>longiss. dorsi</i>	area for longissimus dorsi (including iliocostalis)
<i>cocc. iliac.</i>	area for coccygeo-iliacus (= m. caudæ dorsalis) + iliocaudalis
<i>il. tib.</i>	area for iliotibialis (= extensor iliotibialis I Gadow)
<i>ilic. fem.</i>	area for iliofemoralis
<i>ilio. fib.</i>	" " iliofibularis
<i>pub. tib. + ambiens</i>	" " pubitibialis and ambiens
<i>obl. abd.</i>	" " obliquus abdominis (on processus lateralis pubis)
<i>pub. isch. fem. ext.</i>	" " pubi-ischiotrochantericus externus (= p. i. fem. ext. Gadow)
<i>pub. isch. troch. int.</i>	" " for pubi-ischiotrochantericus internus Osawa (= p. i. femoralis int. Gadow)

<i>rect. abd.</i>	area for rectus abdominis (on epipubic cartilage)
<i>isch. troch.</i>	" " ischiotrochantericus Osawa (= pubi-ischiofemoralis posterior Gadow)
<i>cocc. isch.</i>	area for coccygeo-ischiadicus (Osawa) (= ischiocaudalis Gadow)
<i>isch. tib. post.</i>	area for ischiotibialis posticus Osawa (= Flexor tibialis internus Gadow)
<i>sph. clo.</i>	area for sphincter cloacæ (Osawa) (= Aftermuskeln α , β , γ , etc. Gadow)

B.—Ornithorhynchus. General location of the chief muscle areas of the pelvis. Oblique view from the right side and partly from below. Data chiefly from Coues.

<i>glut. min., glut. med.</i>	areas for the deep gluteal muscles (derived from iliofemoralis)
<i>iliacus, pectineus,</i> <i>ps. min.</i>	} areas for the iliacus pectineus and psoas minor muscles which collectively represent the pubi-ischiofemoralis internus. The psoas minor is attached to the "pectineal process" along with the sartorius.
<i>add. brev.</i>	area for adductor brevis (= ?longus)
<i>add. long. add. mag.</i>	adductor longus, magnus The adductor series probably represents the more peripheral parts of the pubi-ischiofemoralis externus of <i>Sphenodon</i> , while the obturator externus represents the more central part.
<i>pyram.</i>	area for pyramidalis abdominis
<i>rect. fem.</i>	" " rectus femoris (probably derived from ambiens)
<i>quad. fem.</i>	" " quadratus femoris (probably derived from pubi-ischiofemoralis posterior, along with obturator internus and gemmellus inferior)
<i>semitend.</i>	area for semitendinous (probably derived from flexor tibialis externus)
<i>biceps</i>	" " biceps (probably derived from iliofibularis)
<i>semimemb.</i>	" " semimembranosus, derived from flexor tibialis internus (ischio-tibialis)

C.—Cynognathus. Inferred location of muscle areas. Abbreviations as in preceding figures.

PLATE XLVI

General location of the principal muscle areas of the pelvis.

A.—Alligator, data chiefly from Gadow.

B.—Cynognathus, tentative location of areas.

C.—Struthio, data chiefly from Gadow. (Compare text figure 10).

D.—Ornitholestes, tentative location of areas. (Compare text figure 10).

The homology of the true adductor series of *Cynognathus* and mammals with the so-called adductors of birds seems doubtful. The adductors of mammals are more peripheral in position lying external to the obturator externus and derived at least in part from the ischiofemoralis of reptiles. The "adductor magnus" of birds on the contrary arises dorsad to the obturator externus and is beneath the obturator internus.

PLATE XLVII

Moschops capensis Broom. Mounted pelvis and hind limbs (A. M. N. H.), $\times \frac{2}{9}$, with tentative general location and direction of the principal pelvic muscles.

*A*¹.—Right side, lateral aspect.

*A*².—Front view, showing left limb directed outward and backward, right limb outward and forward.

PLATE XLVIII

A series of femora of reptiles and mammals illustrating the morphology of the femoral trochanters. Scales various.

Upper row, proximal view.

Middle row, front (anterosuperior) view.

Lower row, back (posteroinferior) view.

<i>cap.</i>	caput femoris
<i>tr. min.</i>	trochanter minor (lesser trochanter), homologous with
<i>tr. in.</i>	trochanter internus, homologous with
<i>tr. 4</i>	trochanter quartus
<i>tr. mj.</i>	trochanter major (great trochanter)
<i>col.</i>	collum femoris
<i>tr. 3</i>	trochanter tertius
<i>foss. tr.</i>	fossa trochanterica

The most ancient and primitive type is in the center (*Dimetrodon gigas*). This has a deep trochanteric fossa and a high internal trochanteric, or adductor, crest, which probably served for the attachment of the ischiofemoralis (adductors), pubi-ischiofemoralis externus (obturator externus) and pubi-ischiofemoralis internus (iliopsoas + pectineus). At the left of the primitive type is the Therapsid-Mammal series, culminating in the marsupial (*Myrmecobius*) and primitive placental (*Pachyæna*) types, in which the internal trochanteric crest gives rise to the lesser trochanter (for the iliopsoas + pectineus). On the right of *Dimetrodon* is a morphological series leading toward the dinosaurs and showing the derivation of the fourth trochanter (for the insertion of the ischiofemoralis and caudifemoralis) from the internal trochanteric crest.

PLATE XLIX

Ventral view of the coracoid region of (A) *Sphenodon*, (B) *Ornithorhynchus*, (C) *Homo*, showing the location of the principal muscle areas.

In all three cases the true coracoids serve for the origin of the coracobrachialis medius, the c. b. longus and the biceps muscles, while from the epicoracoids of *Sphenodon* and *Ornithorhynchus* arise the subcoraco-humeralis (= coracobrachialis brevis) and the supracoracoideus muscles. The "subcoracoid" centre of mammals is probably a new structure associated with the intracapsular origin of the long head of the biceps.

The supraspinatus muscle of mammals may have been derived either from the scapulohumeralis anterior or from the supracoracoideus of primitive reptiles.

PLATE L

Inner surface of the left half of the pectoral girdle of *Iguana*, *Sphenodon*, *Alligator*, *Echidna*, *Moschops* and *Ornithorhynchus*.

The most primitive conditions in the series are seen in the Permian reptile *Moschops*, which retains all the original elements including the cleithrum and the metacoracoid. The presence of a membranous epicoracoid is indicated by the form and relations of the coracoid in the mounted specimen. *Sphenodon* has lost the cleithrum and the metacoracoid but is otherwise primitive. In *Iguana* secondary vacuities are developed in the coracoid and scapula. In *Alligator* the single coracoid, still pierced by the supracoracoid foramen, is extended transversely; the clavicle is lacking but the epicoracoid is probably represented by the membrana episterno-coracoideus. In *Echidna* and *Ornithorhynchus* the metacoracoid is lost and the epicoracoid, perhaps in adaptation to fossorial habits, becomes thick and well ossified. The coracoid is not perforated by the supracoracoid nerve, which passes through the large secondary opening above the epicoracoid. A vestigial ossicle (X) in a certain immature specimen of *Echidna* has somewhat the position of the metacoracoid but is of very doubtful homology.

Article XVI.—A REVISION OF THE LOWER EOCENE WASATCH AND WIND RIVER FAUNAS

BY W. D. MATTHEW AND WALTER GRANGER

PART V.—INSECTIVORA (CONTINUED), GLIRES, EDENTATA

BY W. D. MATTHEW

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INSECTIVORA (CONTINUED)

AFFINITIES OF EOCENE GROUPS REFERRED TO THE INSECTIVORA

In a preceding section¹ of this revision were reviewed the true primates of the Lower Eocene, genera whose reference to the order appeared either conclusively shown or open to no objections, and also three families which, although referred provisionally to the Insectivora, may also be primates and have been so considered by some authorities. They have been so regarded

¹ 1915. Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 429–483.

tentatively by my colleague Dr. Gregory. Since the publication of that section there has appeared the primate section of Stehlin's great monograph of the Eocene Mammalia of Switzerland¹ — in its scope an authoritative revision of the primates of the Eocene of Europe. Here for the first time an American student can obtain an adequate concept of the Eocene primate fauna of Europe, including, besides full and critical descriptions and admirable illustrations of the described fauna, a great number and variety of new forms. Stehlin points out (*loc. cit.*, p. 1507) that the group of American genera described under the family Apatemyidæ are related to the European Plesiadapidæ, and I believe that there can be no question that they should be included under this family. He regards the Mixodectidæ and Microsyopidæ (p. 1503) as more distantly related and of more doubtful affinities. But he is disposed to regard all three families as primates, although careful to disclaim any positive reference of the American genera until they are more completely known.

Stehlin's main reason for this reference is the indubitable fact that the cheek teeth in all these genera are very different from those of any modern Insectivora and much more like those of Eocene lemuroids in their construction. That this summary is far from doing justice to his able and well considered discussion of the evidence I am well aware, but I think it represents fairly the salient point of his argument and I state it in order to indicate why it does not appear to me convincing. Stehlin does not at all overstate the resemblance. It is very close, especially in certain genera, e. g. *Trogolemur*. We have, in fact, found much difficulty in distinguishing fragmentary jaws of *Trogolemur* from those of *Tetoni*, an unquestioned primate. But this is mainly because the Eocene lemuroids and the three groups under discussion have retained the primitive pattern of molar and premolar teeth without much change. There is a very near resemblance in the teeth among the older Eocene and Paleocene mammals of several different orders and, in consequence, there is hardly one of these primitive genera that has not been referred to two or three different orders so long as it was known solely by the cheek teeth. One would hardly suspect the artiodactyl affinities of *Diacodexis* ("*Trigonolestes*," "*Pantolestes*") from its teeth.² They are much like those of Eocene primates, and they are quite

¹ Stehlin, H. G., 1916. Die Säugethiere des schweizerischen Eocæns. Critischer Catalog der Materialien. 7^{er} Teil, zweite Hälfte. Abh. schweiz. paläont. Ges., XLI, pp. 1299–1552, Pls. xxi–xxii and 82 fig. in text. August, 1916. This second half of section seven deals with the primates excepting *Adapis*, which was already considered in the first half of the section.

² Winge, 1906, Jordfundne og nulevende Hovdyr (Ungulata), E Museo Lundii, III, 1, p. 216, does not admit that "*Pantolestes*" is an artiodactyl. He points out that the teeth do not conform to his theories of cusp evolution and concludes that the artiodactyl characters of the feet are due to parallelism and afford no proof of relationship.

unlike those of any modern Artiodactyla. The same may be said of *Mioclaenus* and *Hyopsodus*, whose affinities with the Condylarthra are indicated by skull and skeleton; of *Tricentes* and other genera of Oxyclænidae, which have been called lemuroid primates but appear to be primitive creodonts; of *Pantolestes*, whose skull and skeleton indicate affinities to the Insectivora although there is little or nothing in the teeth to suggest it; and of various other genera whose true affinities are still provisional. The difficulty is not that these orders were not well separated in the Eocene, but that many of their members retained the primitive dental type with but little change.

All modern Insectivora have departed widely from this type in different lines of specialization, yet with a certain parallelism due to similar adaptive requirements. There is indeed a certain insectivorous type of cheek teeth; but a moment's consideration will show that it is shared by the Insectivora with other insectivorous mammals — most bats for instance, and some marsupials (setting aside the dental formula). But in the Eocene Insectivora, although some have assumed this type, it is not as well developed, and others do not show it at all. The Paleocene Leptictidae are not far removed from the primitive tritubercular type; the Paleocene zalambdodonts are nearer to it than any modern zalambdodont; the Eocene Pantolestidae have teeth like those of primitive creodonts, not at all of the "insectivore type."¹ Even the imperfectly known types which are provisionally referred to Tupaiidae, Talpidae and Leptictidae have teeth much nearer to the primitive tritubercular type than their supposed modern relatives, while *Apheliscus* and other questionable forms are all primitive in cheek teeth.

It is true, however, that the three families under discussion have certain specialized characters found in certain lemuroid primates. A tendency to develop a pair of front teeth either as pincers or gnawing teeth, together with a short deep jaw, progressive reduction of the premolars, etc., is seen in them as also in *Chiromys*, in *Tetoni*us, and to a minor degree in *Omomy*s, *Hemiacodon* and *Necrolemur*. But this is a very common type of specialization, the "diprotodonty" of Osborn, and is more or less characteristic of most modern insectivores, assumed at an early date by all rodents, evolved in the tæniodonts, tillodonts, diprotodont and pseudo-diprotodont marsupials. Early stages of it are seen in other primates besides *Chiromys*, but it is not as characteristic of the order as it is of the Insectivora. The shortening and depth of the jaw, the progressive reduction of the remaining front teeth and of the premolars, the tendency to convert the condyle from

¹ The characters of the skeleton, especially of the limb and foot-bones, are the principal evidence for referring the Leptictidae and Pantolestidae to the Insectivora.

the transverse to the orthal type and the molars into crushing and grinding teeth are associated characters shown in varying degree in all diprotodont specializations and therefore not to be regarded as independent evidence of affinity. I am disposed to believe that the posterior position of the mental foramen is in some instances likewise an associated character of this specialization, although not so uniformly coordinated with the degree of diprotodonty exhibited. (It is very marked in the Pantolestidæ, which do not show any notable diprotodonty; among the soricoids it is most marked in the primitive-toothed genera *Talpa* and *Myogale*, etc.)

In sum, my viewpoint is as follows.

The Plesiadapidæ, Mixodectidæ, and Microsyopidæ are three groups, all of which are characterized by diprotodont specializations of the front teeth and have primitive molars. They do not appear to be especially closely related to each other, nor does the supposed relationship of the first group to *Chiromys* appear to me to rest on any resemblances that may not quite as reasonably be ascribed to parallelism. On the other hand they suggest one or another insectivore group in the front teeth, but the evidence for any real affinity is equally unconvincing. Against any especial affinity with *Chiromys* lies the anatomical evidence of skull, brain, and skeleton characters of the latter, which point to a near affinity to the Indrisidæ in spite of its extreme diprotodonty, and indicate that its divergence from the other Malagasy lemurs is not of very ancient date, not at all probably farther back than the Eocene. It would seem therefore that *Chiromys* must be a parallel but much later specialization from the lemuroid stock than these Eocene "chiromyoids" even if they are lemuroids. Against the insectivore affinities lies the fact that the molars in all three groups are somewhat nearer in construction to certain Eocene genera which are demonstrably primates than they are to any Eocene genera which are demonstrably Insectivora. In each family there are certain inconclusive but independent points of evidence in favor of insectivore affinity. The strongest is in *Mixodectes*, which has an astragalus distinctly of insectivore, and not of primate, type. *Microsyops* has a two-rooted canine, a character of some Insectivora, unknown among primates. *Plesiadapis* has an enlarged upper incisor, curiously suggestive of the soricoids in its construction. But none of this evidence has much weight, save the astragalus, and the Mixodectidæ is the only family that I am disposed to refer to the Insectivora with any degree of confidence. The others are retained there merely on the ground that it is better to place primitive groups of doubtful affinities in a generalized and broadly inclusive order, such as I consider the Insectivora to be, rather than in a more compact specialized order such as the primates.

We have recently secured considerable skeleton material of *Nothodectes*

which adds largely to the evidence for its affinities. A preliminary comparison shows that it is more or less on the border-line between undoubted primates and undoubted Insectivora. It has many suggestions of primate affinity, yet it is certainly not a specialized lemuroid. Until the material is completely prepared and thoroughly studied, it seems better to defer an opinion as to its exact position.

SUPPLEMENTARY OBSERVATIONS UPON THE PLESIADAPIDÆ (APATEMYIDÆ)

Plesiadapidæ Trouessart, 1897

Synonym: APATEMYIDÆ Matthew, 1909

Dr. Stehlin, in his work upon the Eocene primates, gives carefully finished enlarged figures of upper and lower teeth of *Plesiadapis*. These admirable illustrations show that the teeth approach so nearly in construction to those of our Apatemyidæ that no family distinction can at present be maintained. The additional material of *Nothodectes* and of *Phenacolemur* obtained in 1916 confirms this relationship.

PHENACOLEMUR MATTHEW, 1915

Additional specimens of the upper teeth of this genus show the premolars to be two, the fourth being submolariform. The construction of the upper teeth is fundamentally like that in *Nothodectes*, but more progressive. The molars are quadrate, owing to expansion of the postero-internal shelf; the fourth premolar is subquadrate, with a large postero-internal shelf; the metacone (trittocone) is not so widely separated from the paracone ("protocone") as in the molars and is noticeably smaller. The third premolar has no internal shelf or cusp; the main cusp is high, robust, simple, recurved, with small posterior heel, and corresponds very closely to the lower premolar (p_4).

Four specimens were found in the Lower Gray Bull beds on South Elk Creek by Wm. Stein. All belong to the smaller species, *P. citatus*.

An isolated upper incisor from the same locality and horizon as the above specimens is provisionally referred to *P. citatus*. It is much like the large upper incisor of *Nothodectes* (*infra*).

NOTHODECTES MATTHEW, 1915

Additional and more complete specimens of this genus were obtained by Mr. Granger in southern Colorado during the season of 1916. The horizon is the Tiffany beds near Ignacio on the northern boundary of the San Juan

basin, equivalent or nearly so to the Clark Fork beds in the Bighorn basin of Wyoming. A number of upper and lower jaws, some fairly complete, the front of a skull showing the upper molars and premolars, and various skeleton bones have been extracted from the matrix. Preliminary description of the dentition appears in a preceding article in this Bulletin.

The dental formula is $\frac{2.1.3.3}{1.0.2-3.3}$, assuming that the enlarged lower teeth are incisors.

The molar pattern of *Phenacolemur* and *Nothodectes* differs notably from that of *Pelycodus* and its allies in the relations to the protocone of the postero-internal crest or cusp. The "hypocone" is not evolved as a cusp budded off from the protocone, as in the Notharctidæ, nor does it originate from a wholly independent basal cingulum, as Stehlin states is the origin of this cusp in the Adapidæ and as it appears to be in the Tarsiidæ and *Microsyops*. The postero-internal cingulum in *Phenacolemur* and *Nothodectes* makes a broad sweeping curve and joins the tip of the protocone somewhat on its inner face, but the hypocone is apparently developed from the heavy middle portion of the cingulum and is clearly not budded off from the tip of the protocone. *Plesiadapis*, judging from Stehlin's figure, presents conditions intermediate between this and *Pelycodus*.

It appears to the writer that the origin of the hypocone in these various tritubercular types presents a great number of variations. Stehlin has pointed out the distinct origin, in some groups by budding from the protocone, in others arising from the cingulum, and has insisted upon its importance in judging of the affinities of the groups. It would appear at first that these two methods of forming a postero-internal cusp were fundamentally distinct, as indeed Stehlin regards them, and that all "hypocones" must belong to the one type or the other. But the present genus, considered along with *Plesiadapis*, shows conditions that may be regarded as intermediate. In *Plesiadapis* the hypocone is obviously, as Stehlin shows, nearer to the budded type of Notharctidæ, the rudimentary cusp appearing on the line of the peculiarly placed crest that rises to the crest of the protocone, while the true postero-internal cingulum sweeps around the inner and hinder base of the tooth. In *Nothodectes* the crest above mentioned supplies functionally the place of the basal cingulum which is absent, or else may be regarded as itself the true basal cingulum rising internally to the tip of the protocone instead of sweeping around its base. It would not be difficult to cite a series of intermediate stages among tritubercular teeth to support either one of the above interpretations.

Leptictidæ Gill, 1872

The position of the typical group of this family is unquestionably in the Insectivora, with affinities nearest to the Erinaceidæ. *Ictops*, *Leptictis*, *Mesodectes*, *Diacodon*, and *Parictops* pertain to this group, the first three Oligocene, the last two Lower Eocene. It is not known from the Bridger or Uinta. I have provisionally referred to the family a number of genera of uncertain relations. *Didelphodus*, *Phenacops*, and other genera are of very doubtful affinities but can not easily be placed in any other family. They may prove to be creodonts; the skeleton is unknown.

Key to Genera of Leptictidæ

- I. *Leptictinæ*: Upper molars with *pa* and *me* external, hypocone strong; p_4^4 molariform; lower molars with vestigial pa^d or none; p_1 one-rooted.
 - A. Two upper incisors; no sagittal crest but paired lateral crests.
 - 1. P^3 with internal, anteroexternal, and posteroexternal cusps.....*Ictops*
 - 2. P^3 with internal and posteroexternal cusps.....*Mesodectes*
 - 3. P^3 simple, high, compressed.....*Leptictis*
 - B. Three upper incisors; a low sagittal crest but no paired lateral crests.
 - 4. P^3 as in *Ictops*; anterior lower premolars simple. Canines small.

Diacodon
 - 5. Canine larger; incisors minute.....(subgenus) *Palæolestes*
 - 6. Anterior lower premolars broad-bladed with accessory cusps. Canines small.....*Parictops*
- II. *Didelphodontinæ*: Upper molars with *pa* and *me* submedian, broad external shelf, hypocone rudimentary; p_4^4 simple or submolariform; lower molars with strong paraconid.
 - A. Canines moderately large; incisors small; p_1 two-rooted; p_4 with accessory cusps.
 - 7. Three upper premolars.....*Didelphodus*
 - B. Canines large; incisors small; p_1 one-rooted; p_4 unknown.
 - 8. Premolars short, high, crowded.....*Phenacops*

DIACODON COPE, 1875

Type.—*D. alticuspis* Cope from the Wasatch of New Mexico.
Synonym.—*Palæictops* Matthew, 1899, type *Ictops bicuspis* Cope.
Generic characters.—Dentition, $\frac{3.1.4.3}{2.1.4.3}$. P^4 molariform with strong parastyle; p^3 with strong metacone and protocone; p^2 with small metacone. Upper molars and p^4 with well separated, externally placed paracone and metacone; strong hypocone; compressed crescentic protocone. P_4 with large paraconid, otherwise like the molars. Lower molars with high, well

separated, angulate protoconid and metaconid of equal height, heel basined, entoconid smaller than hypoconid, paraconid vestigial; hypoconulid minute except upon m_3 . P_3 with posterior accessory cusp and small heel; p_2 with minute heel, p_1 one-rooted, simple. Canines rather small, the upper oval, of moderate length, one-rooted. Skull with low sagittal crest but no lateral crests.

Diacodon alticuspis certainly belongs to the Leptictidæ, to which Cope referred it in 1885, and is apparently congeneric with *Palæictops*, although based upon a species distinct from *P. (Ictops) bicuspis* of the Wind River. The second species referred by Cope to the genus, *D. celatus*, is of quite different affinities and is provisionally referred to *Nyctitherium*. The generic characters stated above are drawn from *D. bicuspis* and from the referred specimen of *D. alticuspis*.

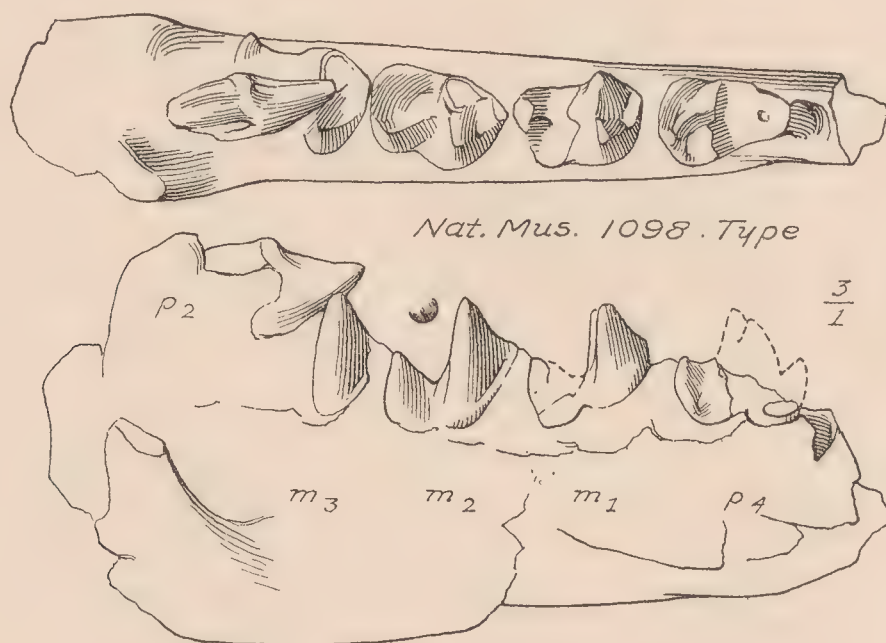


Fig. 1. *Diacodon alticuspis*. Type, U. S. National Museum, from the New Mexican Wasatch. The specimen consists of a part of the right ramus of the lower jaw with p_4 - m_3 more or less damaged and p_2 displaced. External and superior views, three times natural size.

Diacodon alticuspis Cope

Figs. 1 and 2

Diacodon alticuspis COPE, 1875, Syst. Cat. Vert. Eoc. New Mex., p. 12; 1877, Ext. Vert. New Mex., p. 132, Pl. XLV, fig. 19; 1885, Tert. Vert., p. 260.

Type.—U. S. Nat. Mus. No. 1098, lower jaw with p_4 - m_3 and displaced p_2 , most of the teeth badly mutilated and partly buried in matrix. Figure 1.

Specific characters.— $M_{1-3} = 9.5$ mm.; m_1 smaller than m_2 ; depth of jaw beneath $m_3 = 4.7$ mm.

Only one additional specimen (Fig. 2) in the American Museum collections can be certainly referred to this species. This consists of a part of the

skull and jaws of an insectivore, No. 12831, collected in the Wind River Basin in 1904 for the Amherst Museum and presented in exchange to the American Museum through courtesy of Dr. F. B. Loomis. The upper and lower teeth from p_4^4 to m_3^3 are fairly well preserved, although they have been somewhat damaged by weathering and hasty preparation. Parts of the preceding premolars are also shown on the specimen, but the jaws are so locked together and buried in a difficult matrix that I have only partly cleared them, but sufficiently to show that they agree in size and characters with *Diacodon alticuspis* so far as comparisons can be made with the damaged

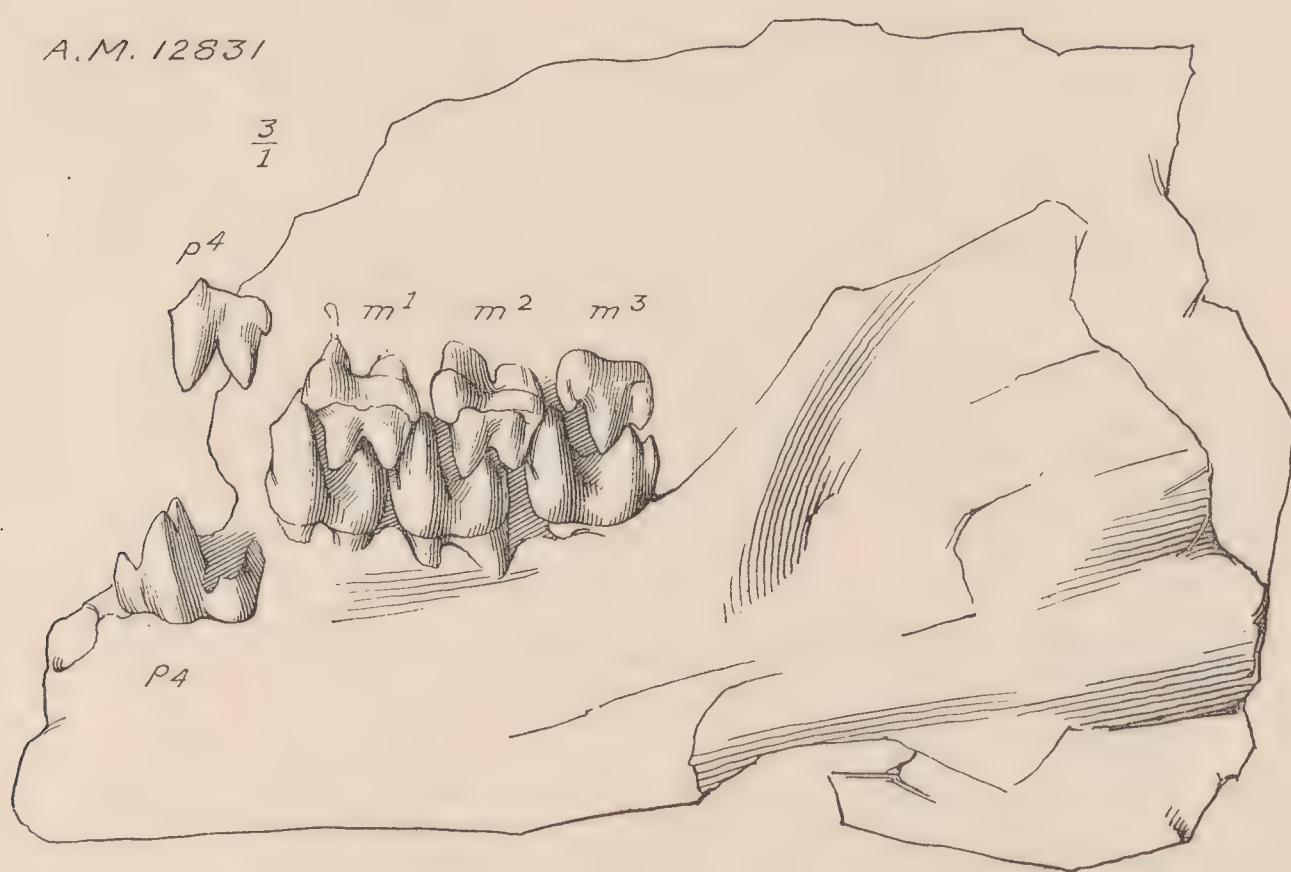


Fig. 2. *Diacodon alticuspis*. Upper and lower jaws from Lysite horizon in Wind River basin, Wyoming; Amer. Mus. No. 12831. Left side view, three times natural size, showing unworn molars and molariform premolar.

lower jaw which is the type of that species. They differ from those of *D. bicuspis* only in the smaller size, less transverse diameter of the upper molars, greater reduction of metacone on m^3 and of heel of m_3 , and other minor characters. The specimen is from the Bridger Creek (Cottonwood Draw) locality in the Wind River Basin, was found by Mr. (Professor) T. C. Brown, and bore the Amherst Museum number 408. It is from the Lysite horizon. The teeth are unworn, the premolars not yet completely erupted from the jaw; the last molar is fully in place. In this genus, as in *Ictops*, therefore, the permanent dentition is very late, replacing the temporary teeth after the skull is fully adult.

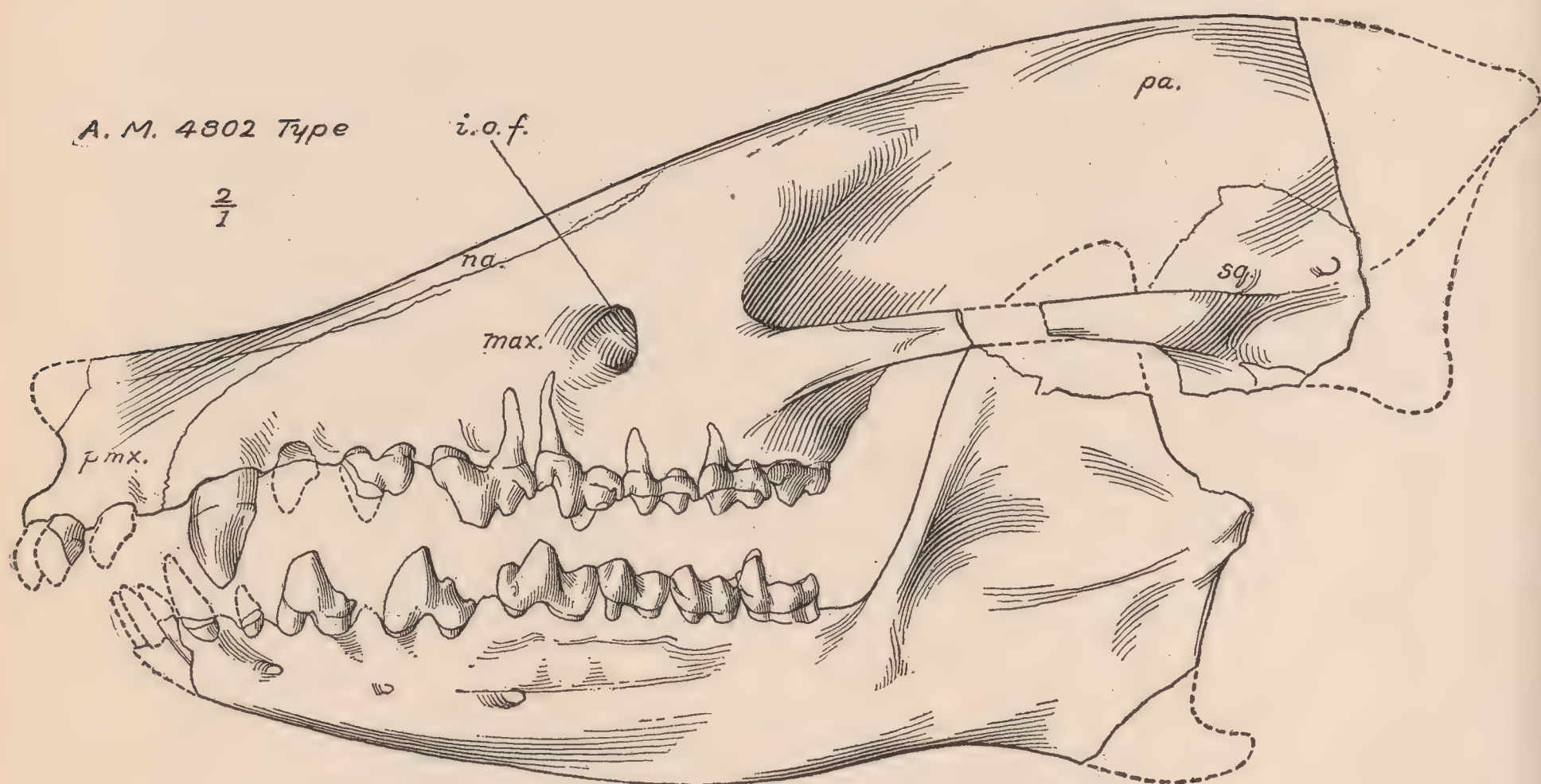


Fig. 3. *Diacodon bicuspis*. Skull and jaws, type specimen, from Lost Cabin horizon in Wind River basin. The original, figured by Cope in Tertiary Vertebrata, is considerably crushed, and has been re-set by the artist. Twice natural size. *I. o. f.*, infraorbital foramen; *max.*, maxillary; *na.*, nasal; *pa.*, parietal; *pmx.*, premaxillary; and *sq.*, squamosal bones.

Diacodon bicuspis (Cope)

Figs. 3-5

Stypolophus bicuspis COPE, 1880, Amer. Nat., XIV, p. 746; (*Ictops*), 1881, Bull. U. S. Geol. Survey Terrs., VI, p. 192; 1885, Tert. Vert., p. 266, Pl. xxixa, figs. 2 and 3. (*Palæictops*), MATTHEW, 1899, Bull. Amer. Mus. Nat. Hist., XII, p. 31.

Type.—Amer. Mus. No. 4802; skull and jaws from Lost Cabin beds of Wind River Basin, Wyoming. The original is considerably crushed,

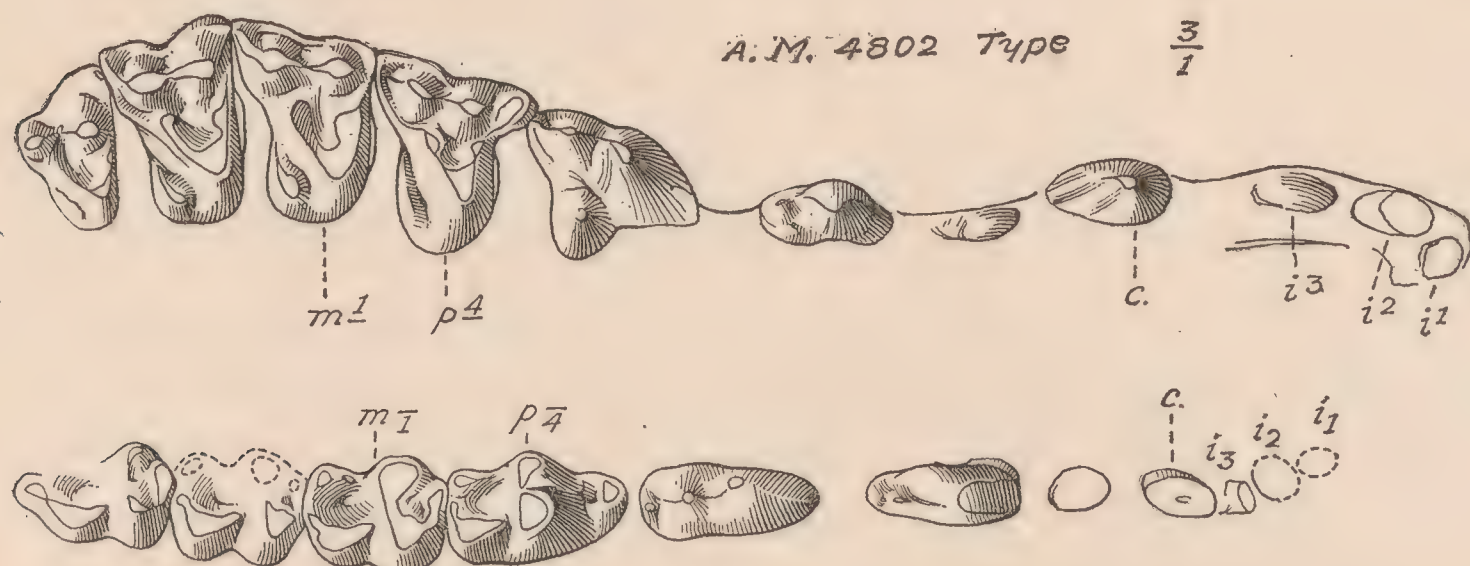


Fig. 4. *Diacodon bicuspis*. Upper and lower teeth. Crown views, three times natural size. From the type skull, Figs. 3-5.

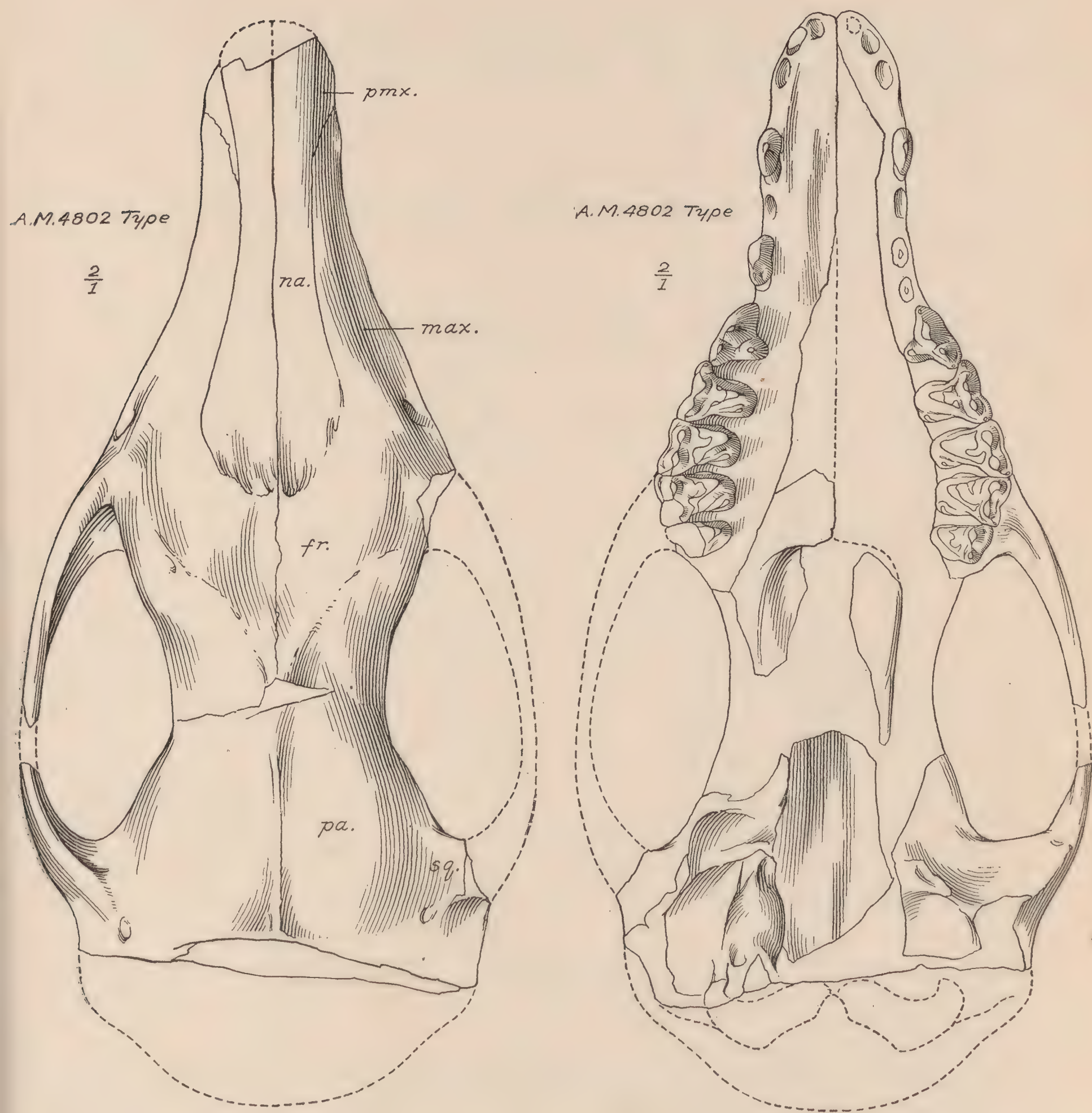


Fig. 5. *Diacodon bicuspis*. Type skull. Top and palatal views, twice natural size. Abbreviations as in Fig. 3.

as is represented in Cope's illustration in 'Tertiary Vertebrata.' In the drawings here published the distortion has been corrected, using skulls of Oligocene Leptictidæ as a guide in reconstruction, with allowance for the very considerable differences in the form and proportions of the cranium.

Specific characters.— $M_{1-3} = 9.5$ mm.; m_1 slightly larger than m_2 ; depth of jaw beneath $m_3 = 6$ mm.

No. 16236, a lower jaw fragment from the Wasatch of New Mexico (? lower beds), and a lower jaw fragment from Willow Creek in the Bighorn Basin (upper Gray Bull level) are referable to this species more nearly than to *D. alticuspis*.

Diacodon* (*Palæolestes*) *puercensis, new subgenus and species

Figs. 6-9

Type.—Amer. Mus. No. 16011; fragmentary skeleton from Torrejon of New Mexico.

Paratype.—Amer. Mus. No. 16748; skeleton from the same locality (not yet prepared).

This species is clearly distinct from any described genus of the Puerco and appears to be a near relative of the Wasatch *Diacodon*. The type specimen (Figs. 6-8) includes the lower jaw and fragments of the upper, but the teeth are all broken off except for p^4 , p_3 and m_3 , which are preserved although not complete. Most of the humerus, femora, and tibiae, with parts of other limb bones, several foot bones including astragali and calcaneum, parts of pelvis, verte-

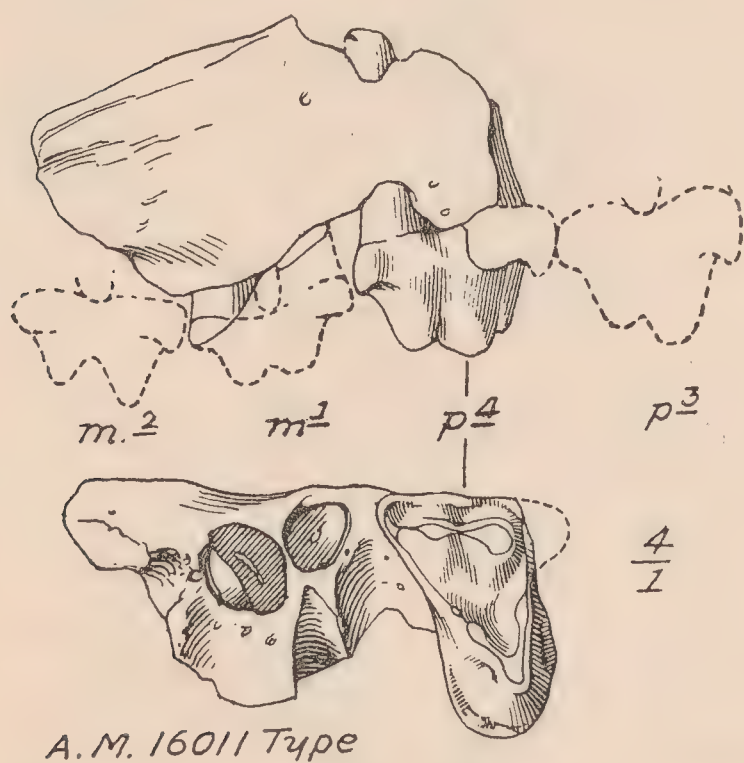


Fig. 6. *Diacodon* (*Palæolestes*) *puercensis*. Upper jaw of type specimen, external and crown views, four times natural size. Upper Paleocene, Torrejon formation, New Mexico.

brae, etc., are present and enable the affinities of the species to be determined. The paratype shows a very perfect upper and lower dentition (Fig. 9).

The teeth agree nearly with those of *Diacodon bicuspis*, except for the large canine and reduced incisors. The upper premolar p^4 is more extended transversely, more compressed anteroposteriorly, the cusps higher and sharper; the metacone, as in *Diacodon* proper, is well separated from the paracone but distinctly smaller. The lower canine root is large, obliquely set, and close to the symphysis; incisors, if present, must have been small and set between the canines as in creodonts, rather than in advance of them as in Insectivora (including *Diacodon bicuspis*). P_1 is small, one-rooted, slightly spaced; p_2 and p_3 are two-rooted, rather short, and high crowned; p_4 is a much longer tooth, considerably longer than any of the molars. The three molars were of nearly equal size; m_3 shows a high but short trigonid,

broken off but evidently with paraconid weak or absent, a long, compressed basined heel, with prominent hypoconulid, hypoconid and two inner marginal cusps. This tooth is quite like that of *Diacodon*, and so are p_4-m_2 . The anterior part of the jaw is somewhat differently proportioned, the premolars shorter, canine larger, and incisors reduced, as compared with *Diacodon* proper. The relationship must, nevertheless, be a very close one, involving a correspondingly close relation in the skeleton of the two genera. As the skeleton of *Diacodon* is unknown, the following description of its Paleocene relative, which will doubtless apply equally to the characters of the Wasatch genus, is given in some detail. The humerus has a small major tuberosity, broad and thick deltoid crest extending nearly half way down the shaft and ending abruptly (but not high and compressed as in *Miacinæ*). The ulna has a long olecranon, sigmoid fossa rather shallow and

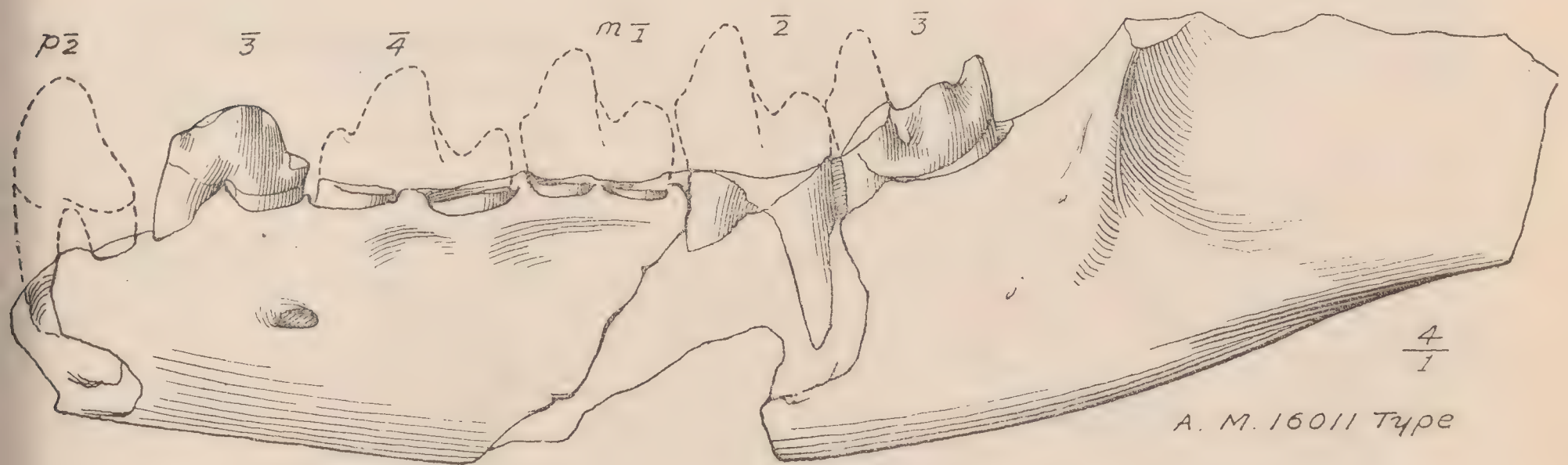


Fig. 7. *Diacodon* (*Palæolestes*) *puercensis*. Lower jaw of type specimen. External view, four times natural size.

very oblique, radial facet flat and indistinctly marked. The femur is very like that of *Ictops*, rather long, the great trochanter expanded posteriorly instead of laterally, trochanteric fossa deep, lesser trochanter posterior, third trochanter an extended marginal rugosity, not prominent. The shaft is of moderate length, the trochlea narrow and elongate, condyles small, not deep. The tibia is as long as the femur or longer, the cnemial crest long, not high, obsolete except at a point about two-fifths down the shaft. The upper part of the shaft is considerably bowed, the lower part straight. The fibula is united to the tibia only at the distal end, the shaft being wholly free, whereas in *Ictops* it is united nearly half-way up. The fibula is broken off and lost from both tibiæ; the internal malleolus is not very heavy; the astragalar trochlear grooves are deep and little oblique. The astragalus has a broad trochlea with prominent equal crests and no astragalar foramen, agreeing with *Ictops* and *Insectivora* generally; the head is broken off but

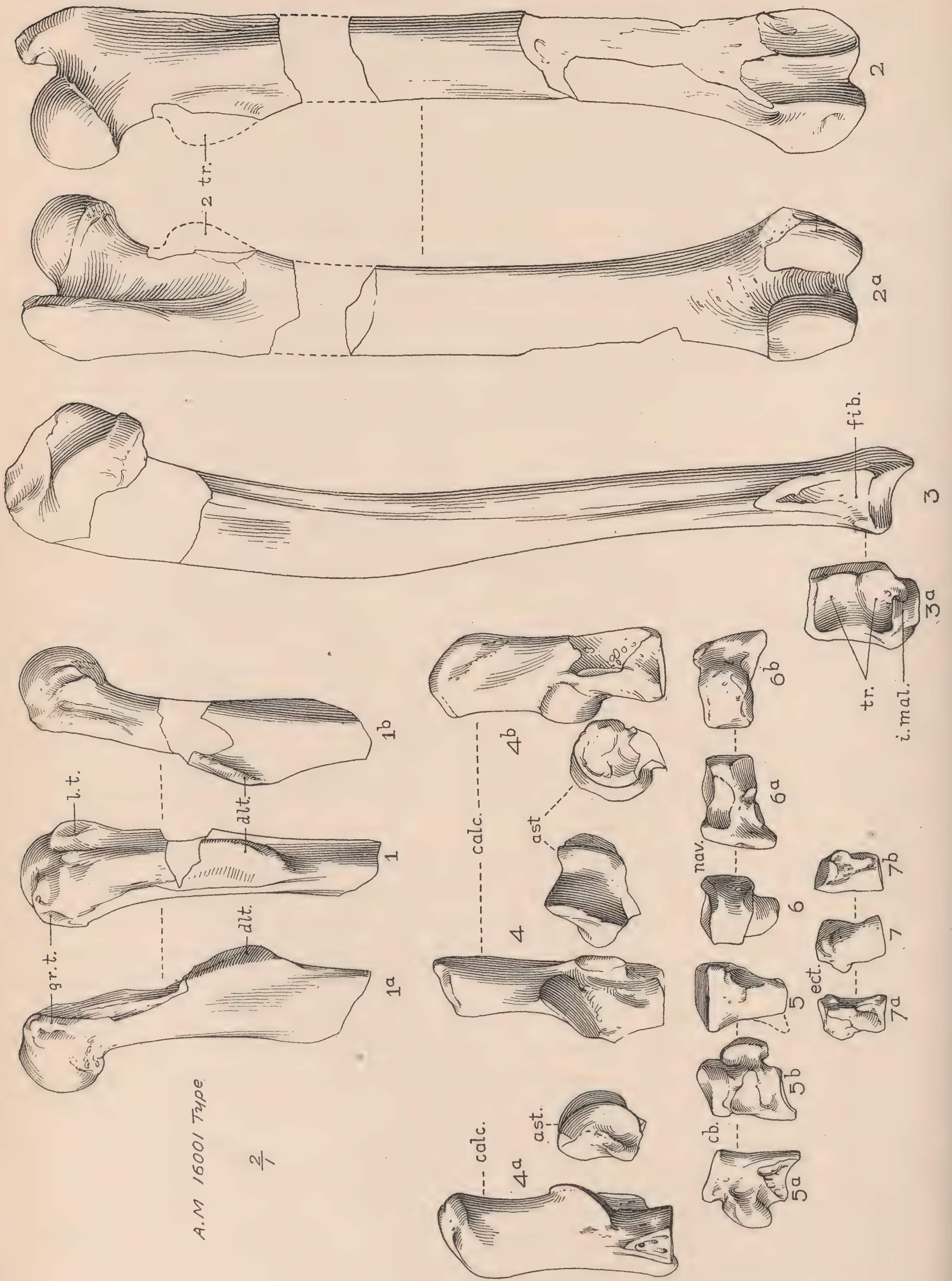


Fig. 8.

the neck is wide and apparently short. The calcaneum has a tuber of moderate length, not compressed; the astragalo-calcaneal facet is smaller and chiefly transverse. There is no fibular facet on the calcaneum. The navicular is rather short, deep, with round-concave facet for the astragalus; deep and strongly concave facet for cuboid; two subequal, flat, triangular distal facets for ecto- and meso-cuneiform; and a strongly convex facet for the entocuneiform, about the same size as the others but facing nearly mesial. The navicular hook is moderately developed. The cuboid has a rather narrow astragalar and broad calcaneal facet, and is of moderate length. No metapodials are preserved, and only one phalanx of the proximal series, short, deep proximally, flattened distally, with the distal facet but slightly convex and facing as much inferiorly as distally. The tarsus agrees in most particulars with that of *Ictops*, but the distal parts of astragalus and calcaneum were considerably shorter and the first digit less reduced.

This species may very well stand as an ancestral type of the leptictine phylum.

PARICTOPS GRANGER

Type.—*P. multicuspis* Granger, 1910, from the Lost Cabin beds of the Wind River Basin.

Distinctive characters.—The lower jaws are like those of *Diacodon* in the molars, but the second and third premolars are peculiarly flattened and trenchant blades with distinct anterior and posterior accessory cusps.

The type of the species is a pair of lower jaws, No. 14741, with p_2 - m_3 well preserved and roots or alveoli of the front teeth. No additional specimens of this genus have been found.

DIDELPHODUS COPE, 1882

Type.—*Deltatherium absarokæ* from the Lower Eocene.

Generic characters.—Dentition, $\frac{?1.3.3.}{3.1.4.3.}$. Upper molars compressed, triangular; paracone and metacone well separated, with a broad shelf external to them, extended at the external angles except the posteroexternal

Fig. 8. *Diacodon (Palæolestes) puercensis*. Parts of skeleton of type specimen. All twice natural size. 1) proximal half of right humerus, anterior view; 1a, external, 1b, internal views; *dlt*, deltoid crest, *gr.t.*, *l.t.*, greater and lesser tuberosities. 2) left femur, anterior view; 2a, posterior view; 2tr., second trochanter. 3) left tibia, external view; 3a, distal end; *tr.* trochlea, *i.mal.*, internal malleolus. 4) astragalus and calcaneum, superior view; 4a, external, 4b, internal views. 5) 5a, and 5b, corresponding views of cuboid; 6) 6a, 6b, of navicular; 7) 7a, 7b, of ectocuneiform.

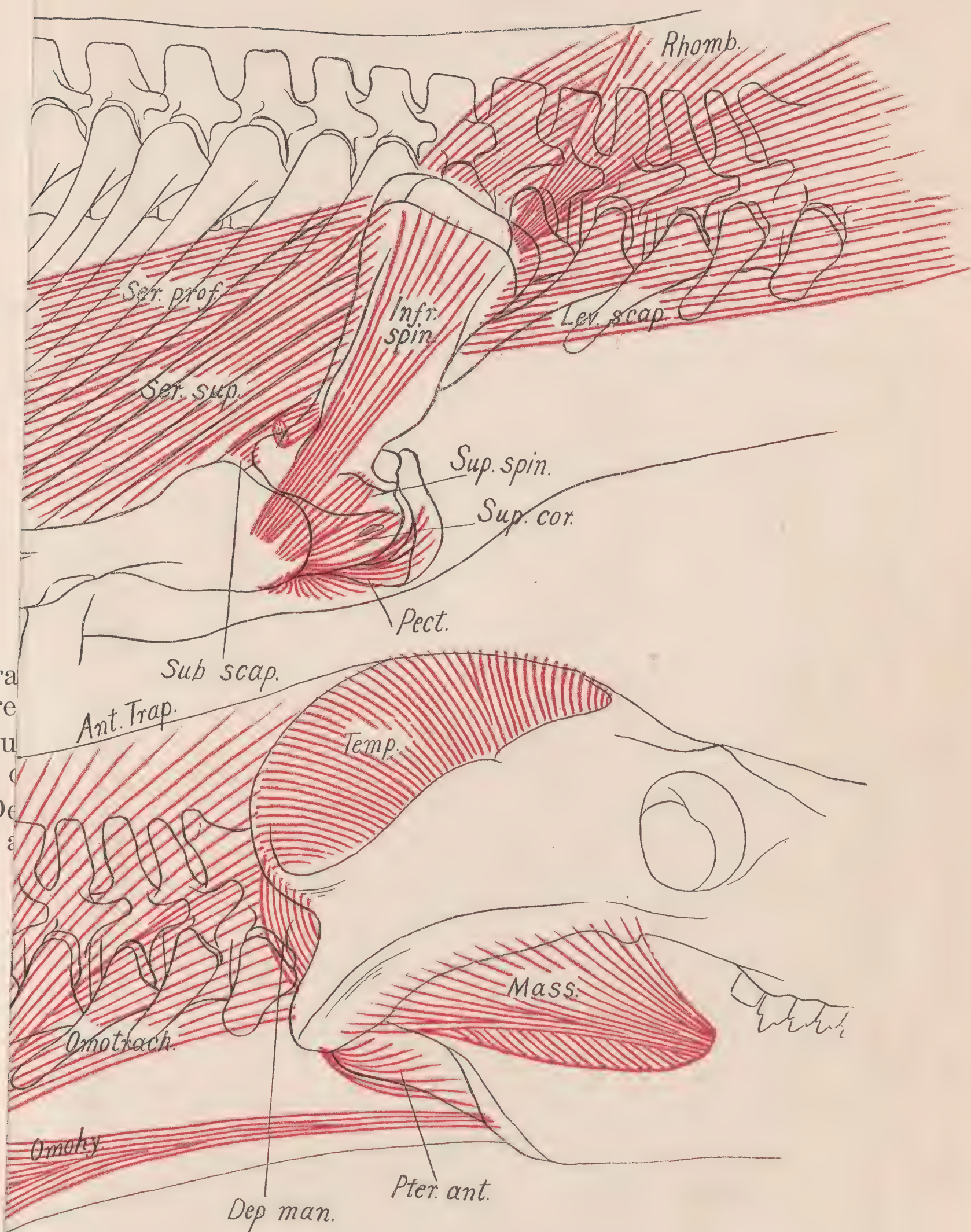


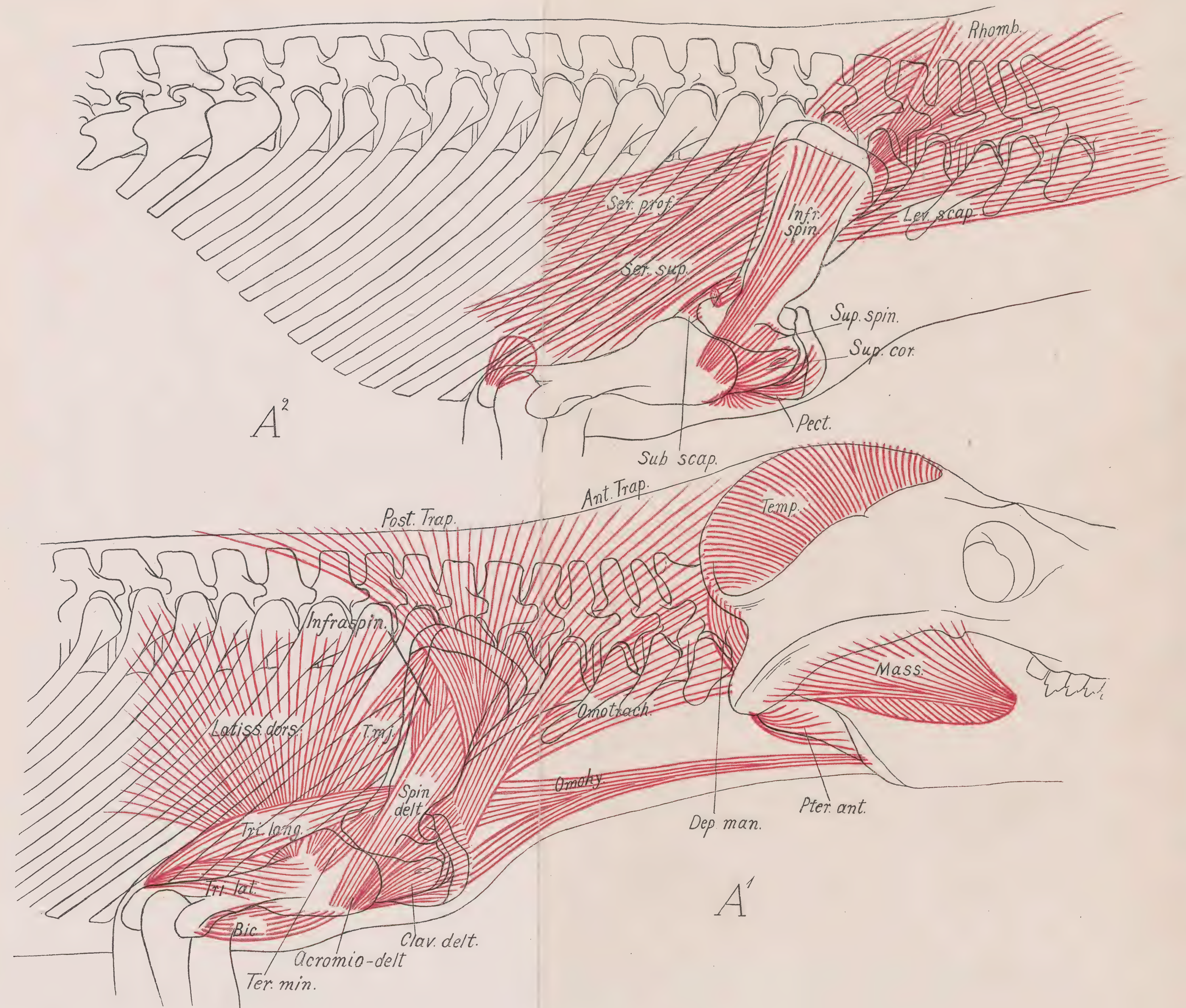
Diagram
pectoral re
A¹—Su
sphincter o
A²—De
trapezius a

A¹

Diagrams showing the probable position of the chief muscles of the pectoral region in *Cynognathus*.

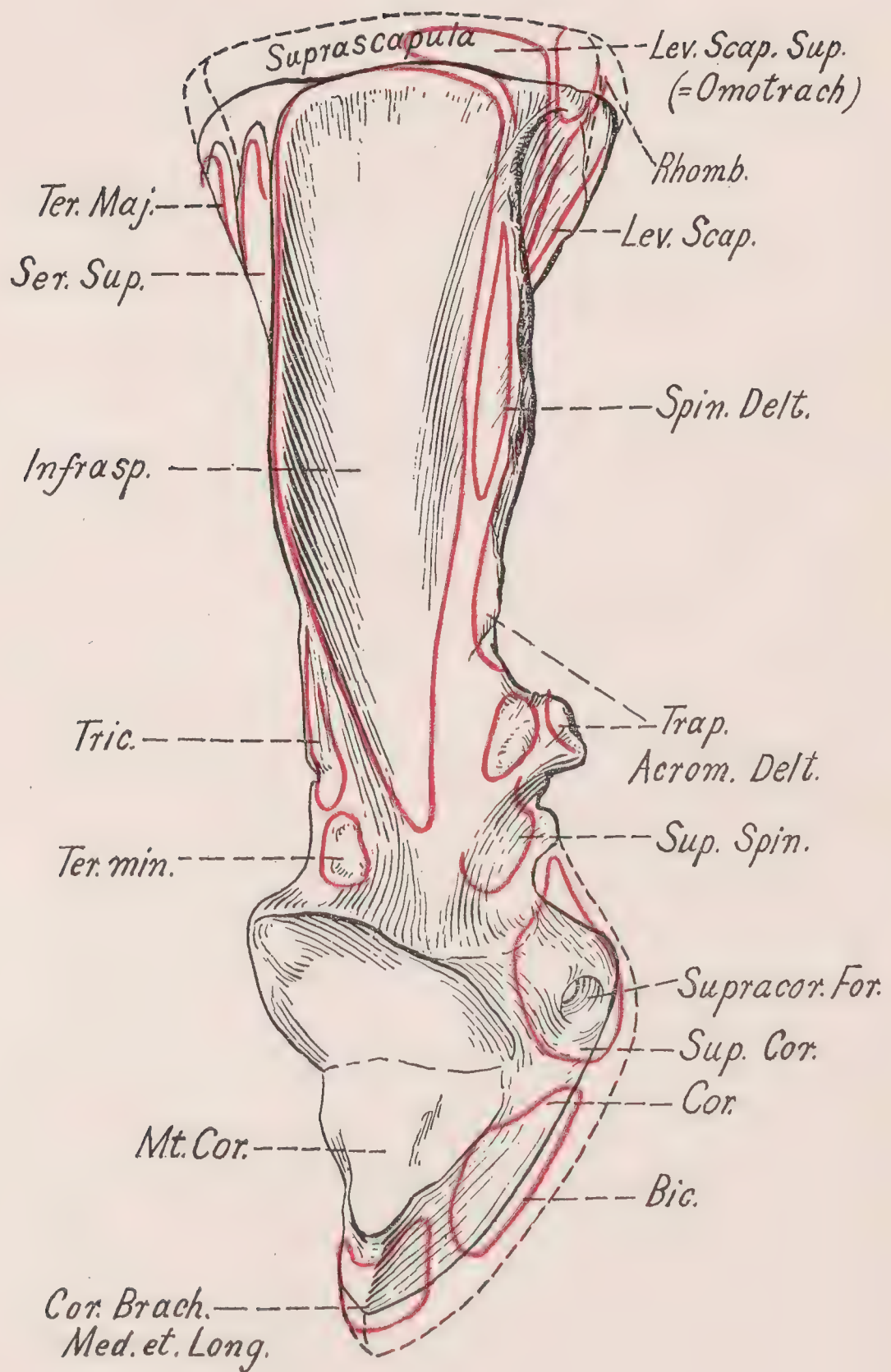
A¹—Superficial muscles after the removal of the skin and of the sphincter colli.

A²—Deeper muscles after the removal of the sphincter colli, trapezius and latissimus dorsi.



ap.

prof.

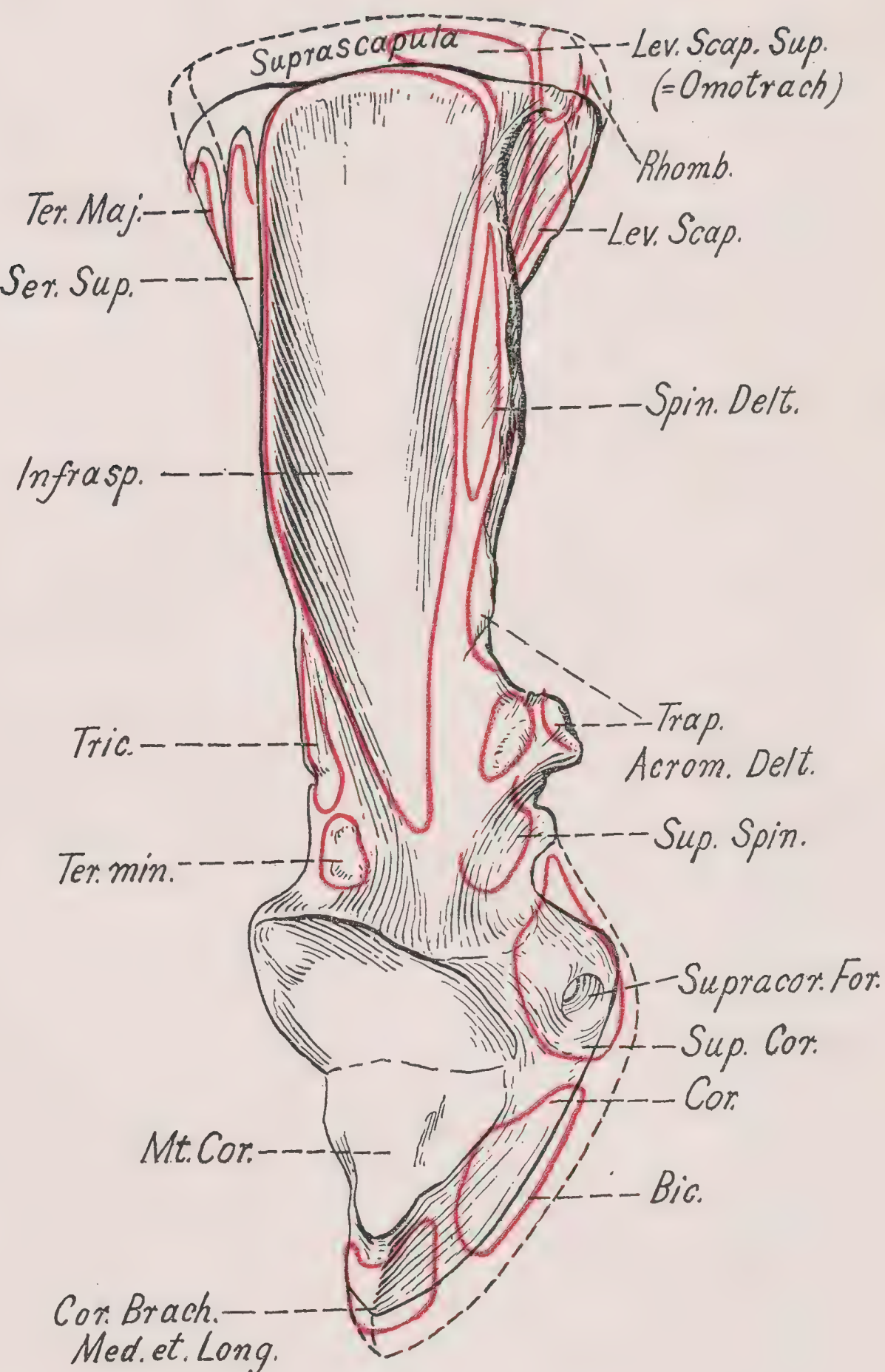
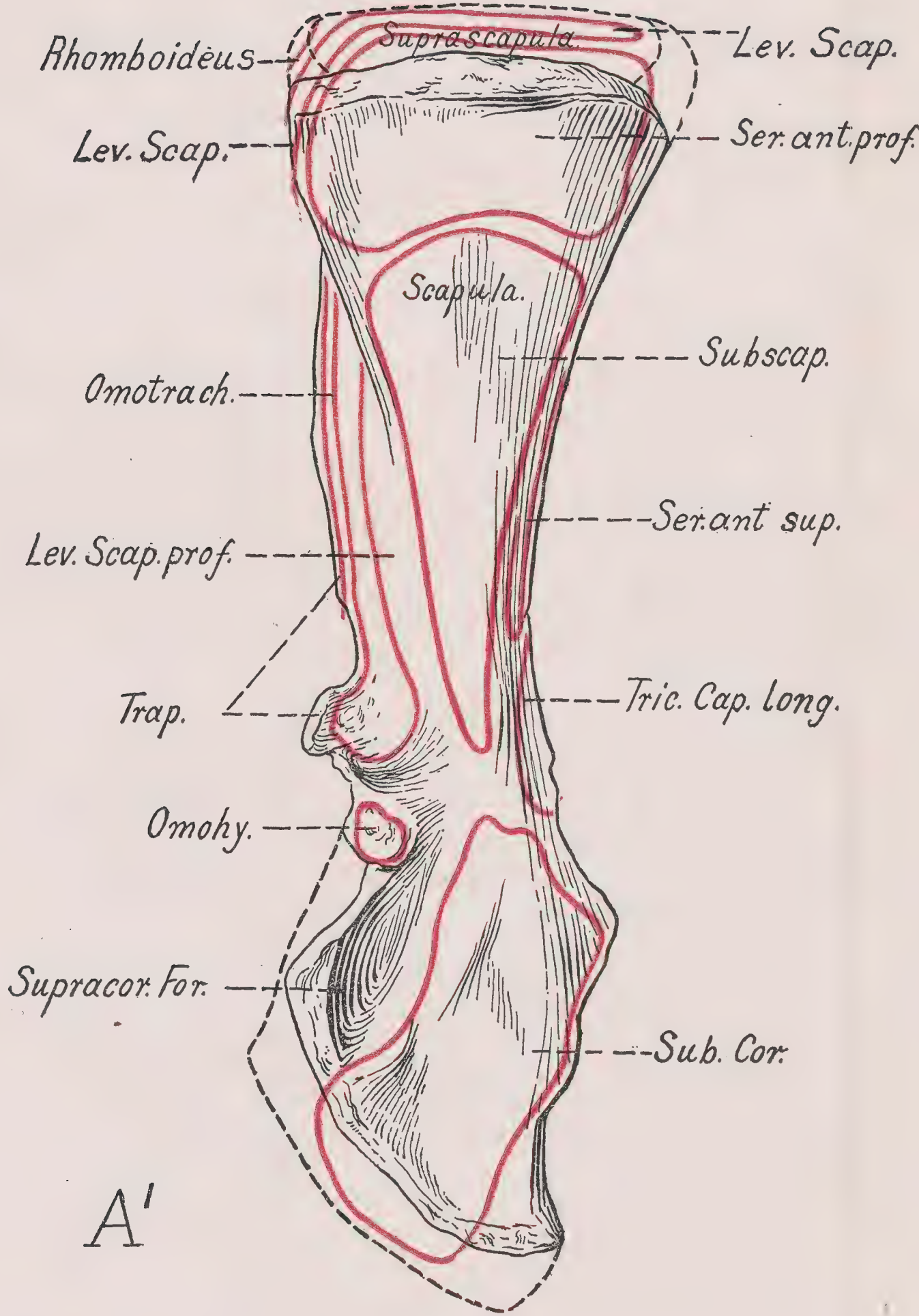


A²

Scapulocoraco-metacoracoid of *Cynognathus crateronotus* (cast of original specimen) with the probable muscle areas.

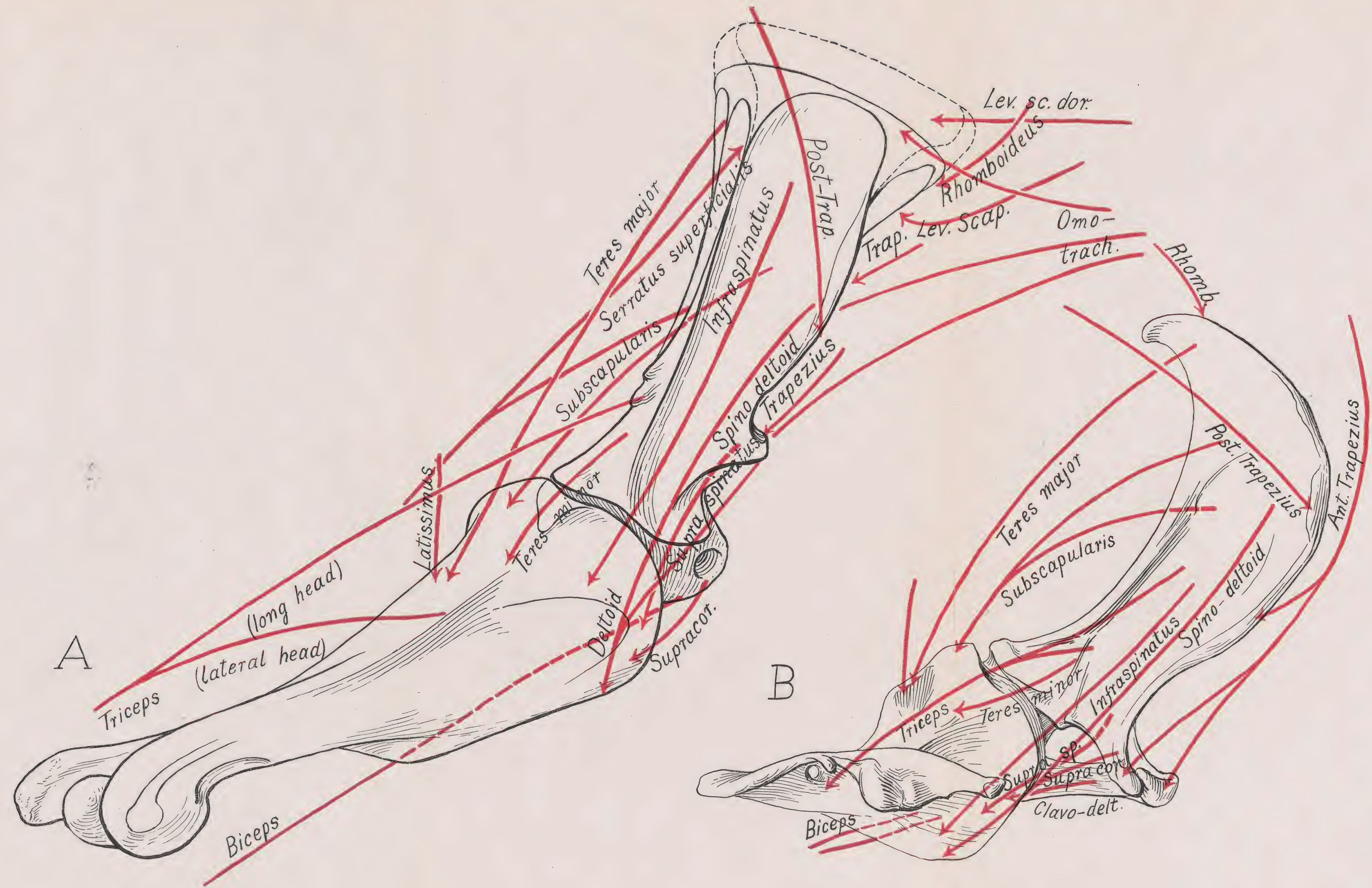
A¹—Medial aspect. A²—Lateral aspect.

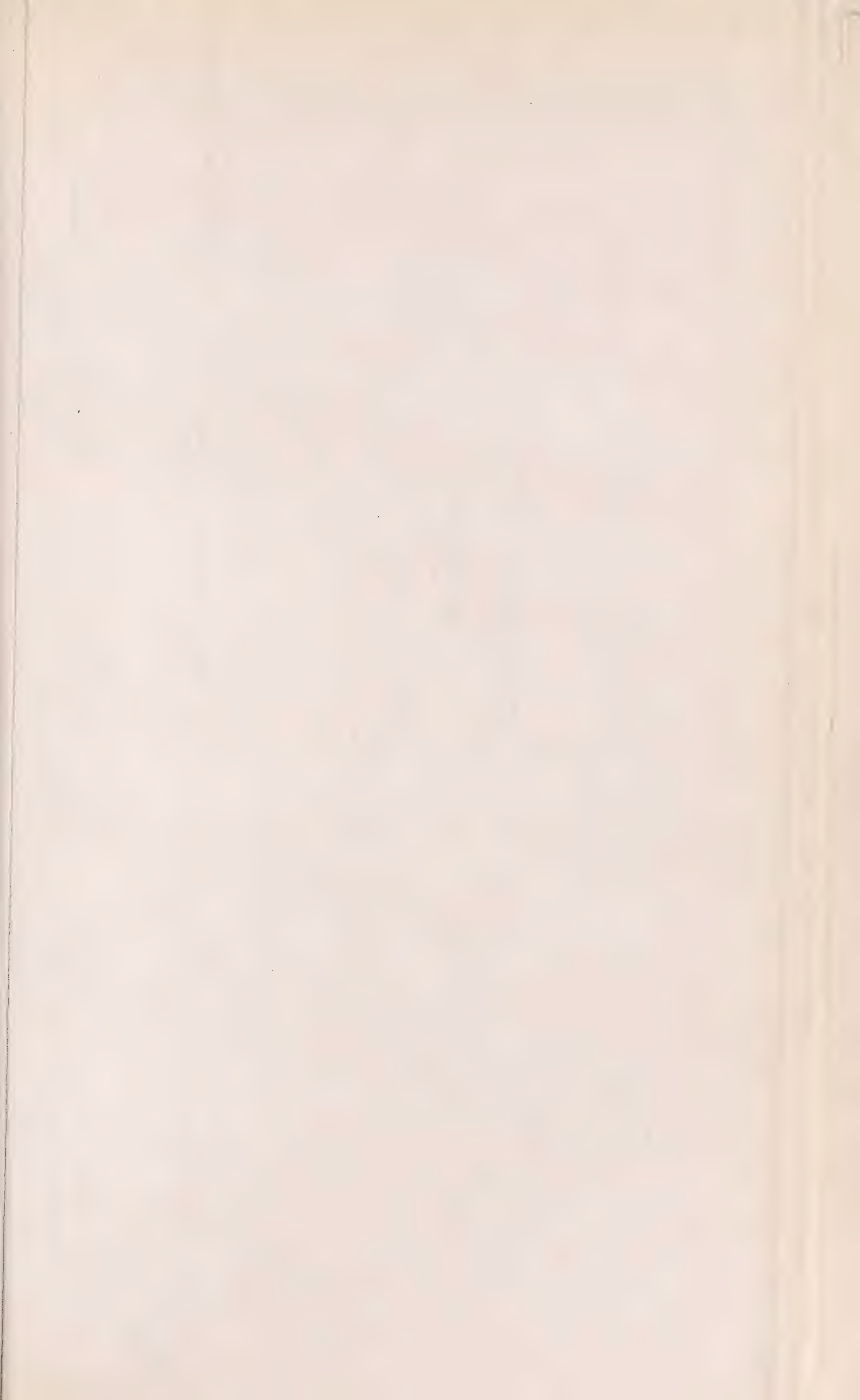
This region is on the whole much more like that of *Ornithorhynchus* than like those of either *Sphenodon* or *Alligator*. The omotrachelian (= levator scapulæ superficialis superior of *Sphenodon*) had a wide area on the cranio-medial surface of the reflected anterior border (= spina scapulæ). The post-spinous fossa was probably occupied by a large infraspinatus (= scapulohumeralis posterior?). This muscle, however, according to Fürbringer, is not the homologue of the similarly placed scapulohumeralis posterior of *Sphenodon*, but has been derived from the supracoideus (epicoracohumeralis), a part of which is supposed to have migrated dorsally and crowded out the scapulohumeralis posterior. In that case the latter may possibly be represented by the infraspinatus secundus of ungulates. The teres minor may have been inserted on a small rugosity above the glenoid fossa; it may represent part of a reduced dorsalis scapulæ, the spino-deltoid representing the other part.



sh
Or

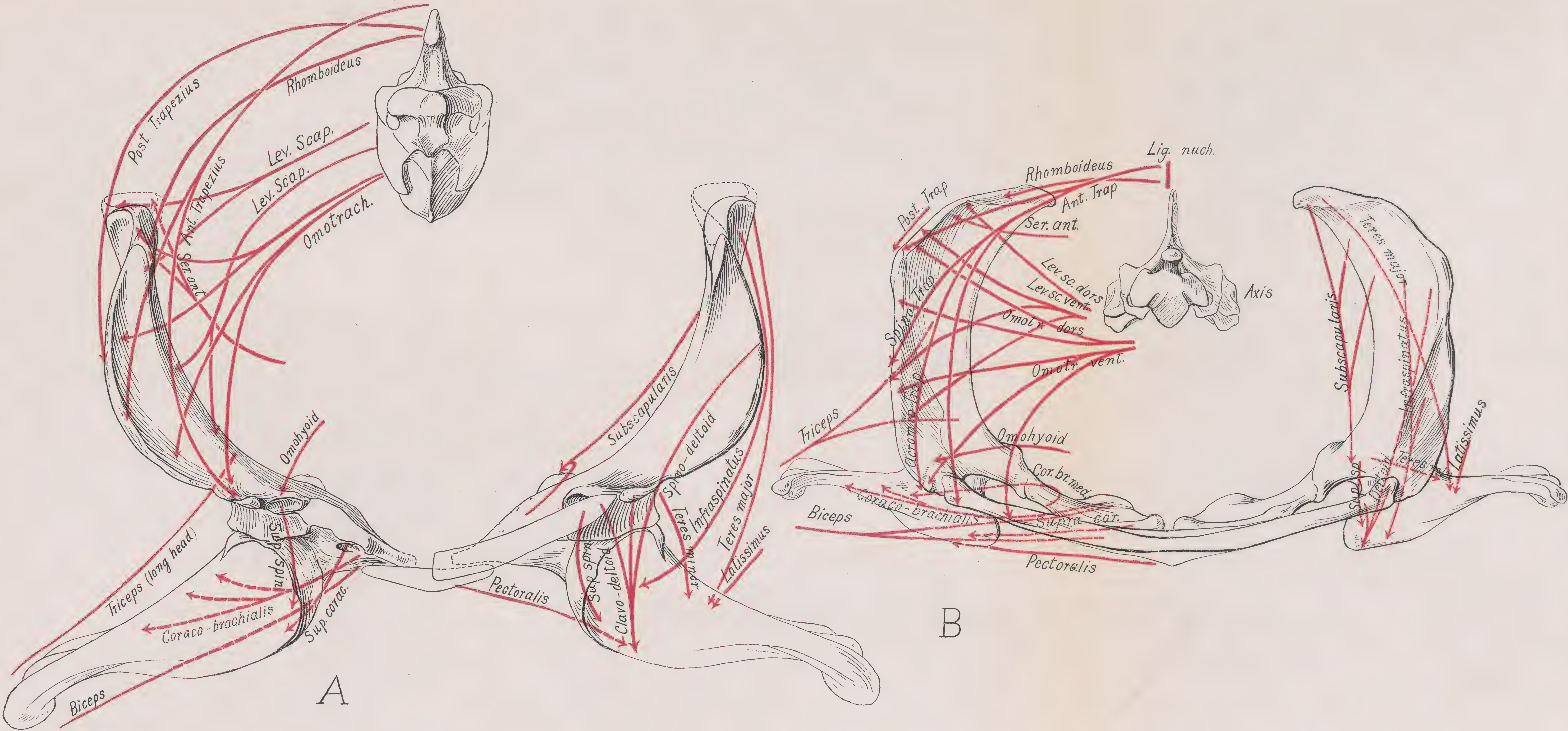
Inferred general position and relations of the chief muscles of the shoulder region in *Cynognathus* (A) as compared with the known facts in *Ornithorhynchus* (B). Right side, lateral aspect.





Inferred general position and relations of the muscles of the pectoral girdle in *Cynognathus* (A) as compared with the known facts in *Ornithomynchus* (B). Front view.

In *Cynognathus* the right clavicle is omitted in order to expose the muscles beneath and behind it. The width across the opposite acromia is conjectural. The suprascapulæ as restored are probably much too small.



-ischiofemoralis internus, part I.

ed by the obturator nerve which is seen passing between the
ischium (*Sy. i.*)

-ischiofemoralis externus
ofemoralis

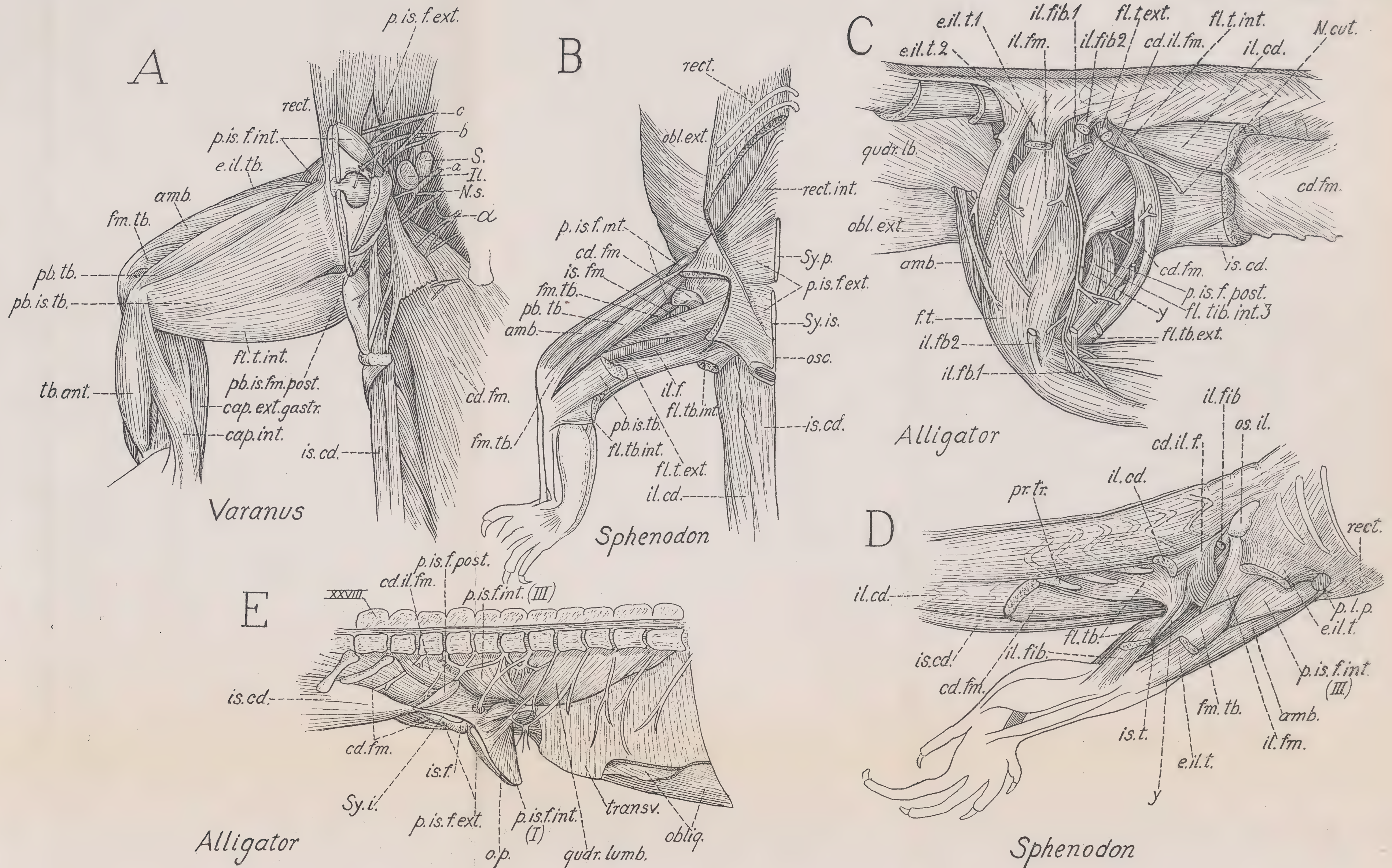
-ischiofemoralis internus, part III, arising from the inner surface of the
th, 25th and 26th vertebræ. Medial to this muscle is the plexus **sacralis**.

-ischiofemoralis posticus

li-iliofemoralis

ifemoralis, attached to the chevrons

ocaudalis



Musculature of the pelvic limbs of recent reptiles. After Gadow.
A.—*Hydrosaurus* (*Varanus*) *marmoratus*. Medio-ventral aspect of the right hind limb with oblique medial view of the right half of the pelvis and associated muscles. After Gadow, 1882, Fig. 36.

S, Il. sacro-iliac articulation (disconnected).
a, b, c, plexus cruralis (first, second, third presacral nerves).

Of these, c gives a branch to the ambiens and another to the iliofemoralis; b contributes largely to the obturator nerve, which traverses the obturator foramen in the pubis. The sacral nerve (NS) is the nerve that issues between the two sacral vertebrae; its plexus (Pl. ischidicus s. sacralis) sends branches to the caudi-iliofemoralis, the caudifemoralis and the publi-ischio-tibialis and the femorotibialis (Gadow, 1882, Taf. XVII, Fig. 16).

The plexus pudendus (a) sends branches to the cloacal and perineal region, and to the caudifemoralis.

rect.	rectus abdominis
p. is. f. int.	pubi-ischiofemoralis internus, arising on inner surface of pubis and ischium
p. is. f. ext.	pubi-ischiofemoralis externus, arising on outer surface of pubis and ischium and seen through the thyroid fenestra
e. il. tb.	extensor iliotibialis
amb.	ambiens
fm. tb.	femorotibialis
pb. tb.	pubitibialis
pb. is. tb.	pubi-ischiofemoralis
tb. ant.	tibialis anticus
cap. int.	gastrocnemius
cap. ext. gastr.	
fl. t. int.	flexor tibialis internus
pb. is. fm. post.	pubi-ischiofemoralis posterior
is. cd.	ischio-caudalis
cd. fm.	caudifemoralis

B.—*Hatteria* (*Sphenodon*) *punctata*. Right pelvic region, ventral view. After Gadow, 1882, Fig. 40. Portions of the rectus abdominis ventralis and of the publi-ischiofemoralis have been cut away to show the underlying muscles.

rect.	rectus abdominis (ventralis)
rect. int.	rectus internus abdominis
Sy. p., Sy. is.	symphysis pubis, symphysis ischii
p. is. f. ext.	pubi-ischiofemoralis externus
os. c.	os cloacae
ic. cd.	ischio-caudalis
p. is. f. int.	pubi-ischiofemoralis internus, part III (inserted on the anterior and partly on the inner surface of the femur)
cd. fm.	tendon of the caudifemoralis near its insertion distal to the external trochanter
is. fm.	ischiofemoralis
fm. tb.	femorotibialis
pb. tb.	pubitibialis
amb.	ambiens
fl. tb. int.	flexor tibialis internus
pb. is. tb.	pubi-ischiofemoralis
fl. t. ext.	flexor tibialis externus
il. f.	iliofemoralis

C.—*Alligator mississippiensis*. Pelvic region, lateral aspect. After Gadow, 1882, Fig. 34.

quadr. lb.	quadratus lumborum, extending downward and backward towards its insertion on the femur
obl. ext.	obliquus externus abdominis

amb.	ambiens, piercing quadratus lumborum on its way toward insertion on the ilium
e. il. tb. 1, e. il. t. 2	first and second branch of the extensor iliotibialis

The nerves in this region come from the crural plexus.

il. fm.	iliofemoralis
f. t.	femorotibialis

The long nerve behind the femorotibialis is the nervus obturatorius.

il. fb. 1, il. fb. 2	iliofibularis, parts 1, 2
f. t. ext.	flexor tibialis externus
f. t. int.	flexor tibialis internus
cd. il. fm.	caudi-iliofemoralis
cd. fm.	caudifemoralis
y.	tendinous branch of the caudifemoralis running to the caput fibulae
is. cd.	ischio-caudalis
N. cut.	cutaneous branch from the sacral plexus

D.—*Hatteria* (*Sphenodon*) *punctata*. Right side, latero-dorsal aspect, after the removal of sections of the extensor iliotibialis, iliofibularis and iliocaudalis. After Fürbringer, 1882, Fig. 39.

os. il.	ilium
il. fib.	iliofibularis
cd. il. f.	caudi-iliofemoralis
	long tendon of caudi-iliofemoralis
il. cd.	iliocaudalis
pr. tr.	transverse processes, above which run the segmental dorsal muscle of the tail (M. caudæ dorsalis)
cd. fm.	caudifemoralis
rect.	rectus abdominis
p. l. p.	processus lateralis pubis
e. il. t.	extensor iliotibialis (connecting anteromedially with the thin tendon of the pubi-ischiofemoralis internus, part I)
p. is. f. int. (III)	pubi-ischiofemoralis, part III
amb.	ambiens
il. fm.	iliofemoralis
fm. tb.	femorotibialis
is. t.	ischiotibialis
fl. tb.	flexor tibialis (internal head)

E.—*Alligator mississippiensis*. Sagittal section of the pelvic region, medial aspect. After Gadow, 1882, Fig. 33.

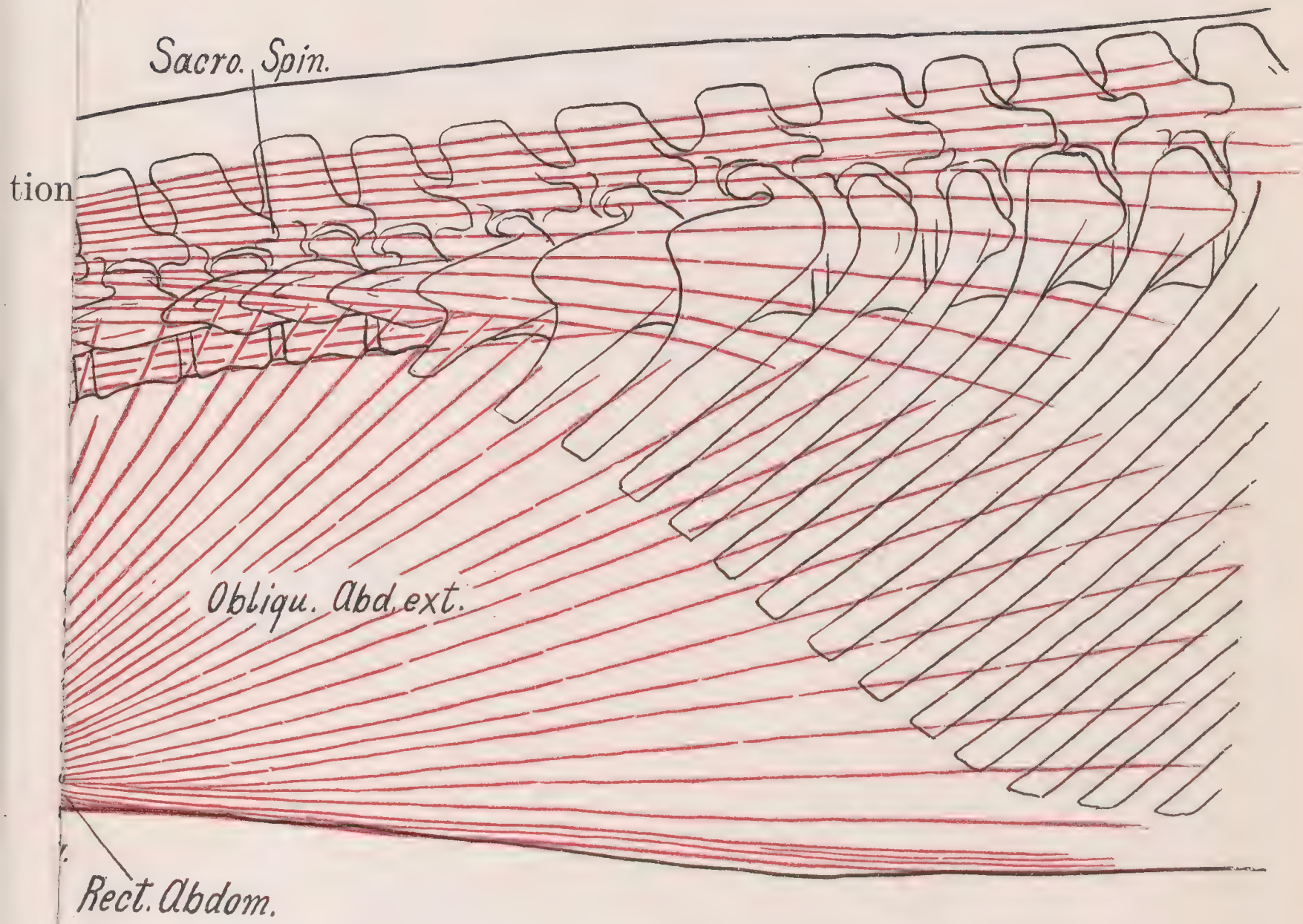
obliq.	obliquus abdominis
transv.	transversus abdominis
quadr. lumb.	quadratus lumborum

The segmental nerves in this region form part of the plexus cruralis.

p. is. f. int. (I)	pubi-ischiofemoralis internus, part I.
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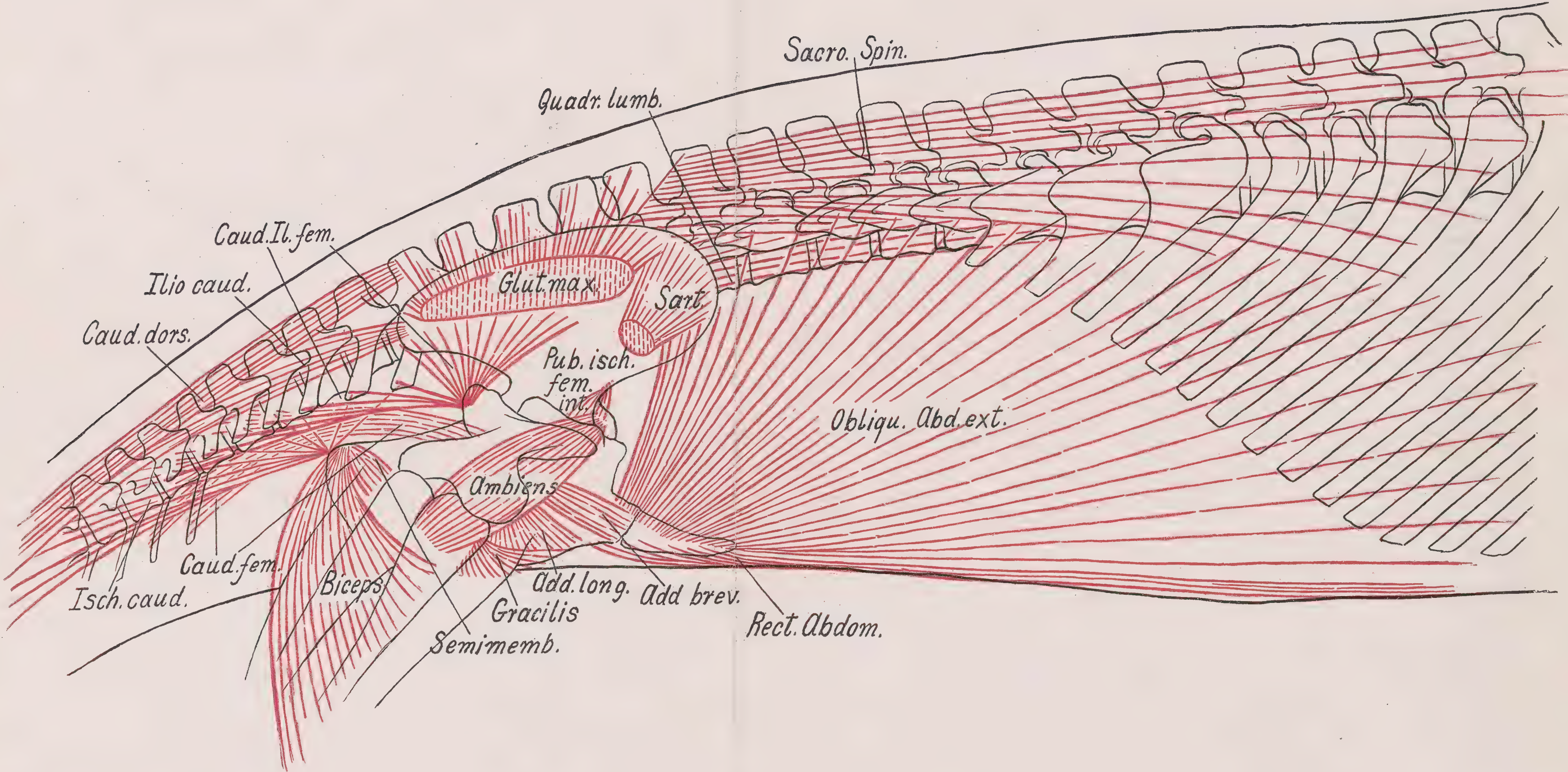
This part is pierced by the obturator nerve which is seen passing between the os pubis (o. p.) and the ischium (Sy. i.)

p. is. f. ext.	pubi-ischiofemoralis externus
is. f.	ischiofemoralis
p. is. f. int. (III)	pubi-ischiofemoralis internus, part III, arising from the inner surface of the 24th, 25th and 26th vertebrae. Medial to this muscle is the plexus sacralis.
p. is. f. post.	pubi-ischiofemoralis posticus
cd. il. fm.	caudi-iliofemoralis
cd. fm.	caudifemoralis, attached to the chevrons
is. cd.	ischio-caudalis



First trial diagram showing the inferred general location and relations of the principal muscles of the pelvic region in *Cynognathus*.

sacro. spin.	sacrospinalis
quadr. lumb.	quadratus lumborum. This muscle may have extended further ventrally and might have even been attached to the upper part of the femur as in the alligator
obl. abd. ext.	obliquus abdominis externus, inserted on the epipubic bones
sart.	sartorius, derived from anterior part of extensor iliotibialis, part X
glut. max.	ectogluteus—tensor fasciæ derived from posterior part of extensor iliotibialis
pub. isch. fem. int.	pubi-ischiofemoralis internus (= psoas major + iliacus + pectineus). Probably much larger than as shown here
ambiens	ambiens (rectus femoris). The rest of the quadriceps (femorotibialis) is not shown
caud. il. fem.	caudi-iliofemoralis (giving rise to deep glutei, pyriformis, etc.)
caud. fem.	caudifemoralis, inserted on postero-medial surface of femur
caud. dors.	M. caudæ dorsalis (extensors)
ilio. caud.	iliocaudalis (abductor caudæ dorsalis)
isch. caud.	ischiocaudalis (abductor caudæ ventralis, coccygeus)
add. brev.	adductor brevis (= part of pubi-ischio-femoralis)
add. long.	adductor longus (= part of pubi-ischio-femoralis)
gracilis	(?derived from pubi-ischiotibialis)
semimemb.	semimembranosus (?derived from ischiotibialis)
biceps	?derived from iliofibularis



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Pub. isch. tib. (=Gracilis)

Cocc. iliac.

Ilio. fib.
(=Biceps)

Ilio fem.
(=Glut. med. + min.)

Long. dors.

Il. tib.

Isch. troch.

Cocc. isch.

Pub. tib. + Ambiens

Obl. abd.

p. l. p

Isch. tib. post.
(=Biceps + Semimemb.
clo.)

Pub. isch. fem. ext.
(=Obt. ext.)

Pub. isch. tib.
(=Gracilis)

A²

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Il. tib. ext. (=Gl. max.)

Il. caud.

Il. fem.
(=Gl. med. + Gl. min.)

Il. tib. int.
(Tens. fasc.)

Caud. il. fem.
(=Pyrif.)

Pub. isch. troch. int.
(=Pect. + Iliac. + Pso. maj.)

Isch. troch. (=Pub. isch. fem. post.
(=Obt. int. + Quad. fem.
+ gemelli)

Biceps

Ambiens + Sart.

Obt. ext.

Obt. for.

Add. brev.

Obl. abd. ext.

Add. mag.

Add. long.

Rect. abd.

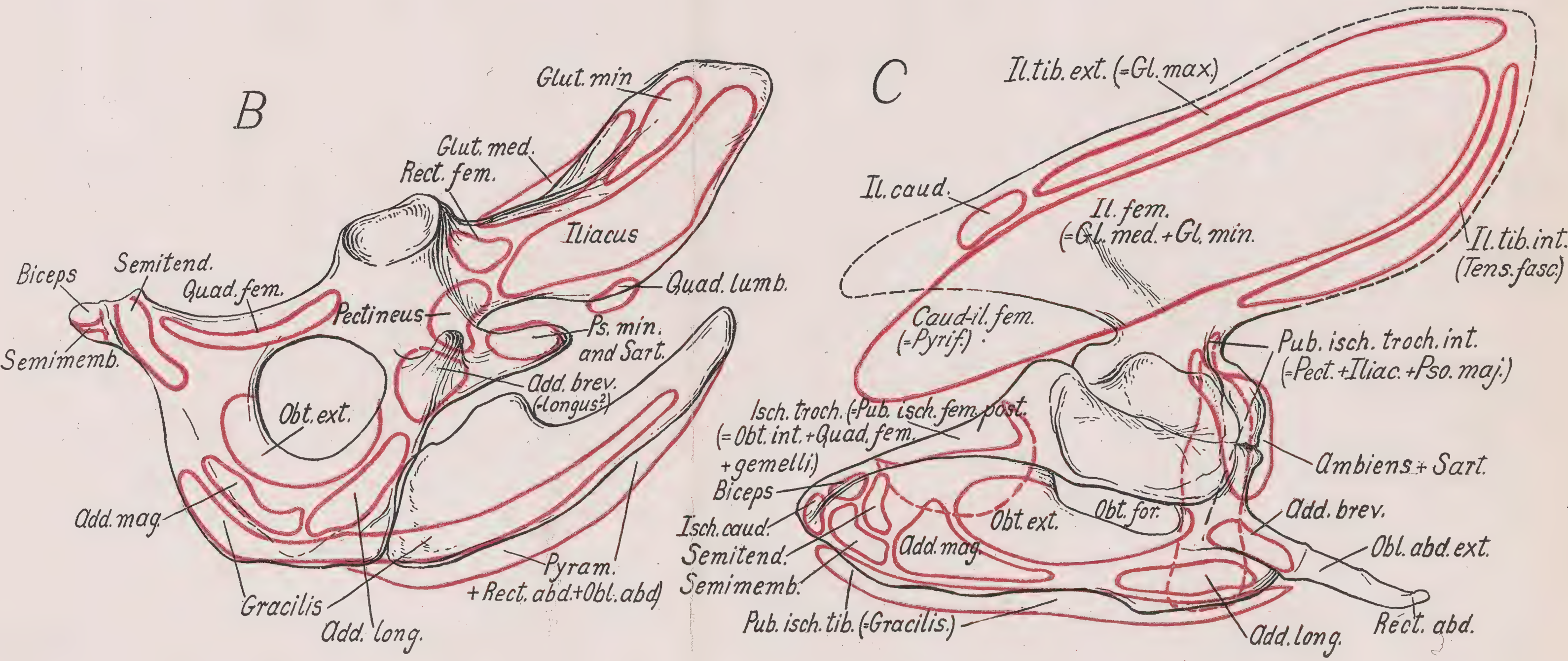
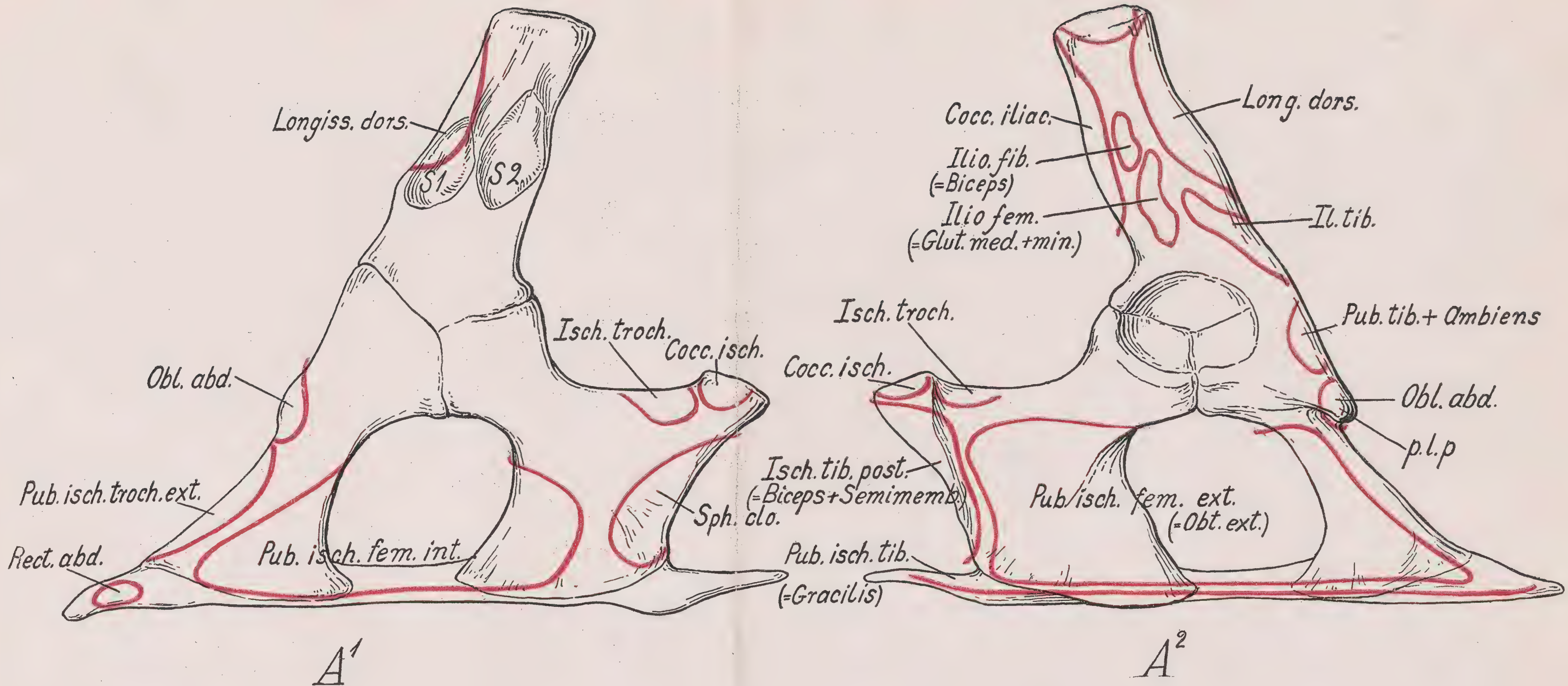
General location of the muscle areas of the pelvis of *Sphenodon* (*A*¹, *A*²), *Ornithorhynchus* (*B*) and *Cynognathus* (*C*). (Compare Plate XLVI.)
*A*¹—*Sphenodon*, right half of pelvis, medial aspect. Muscle areas according to Osawa (1898) and Gadow (1882).
*A*²—The same, lateral aspect. Muscle areas according to Osawa and Gadow.

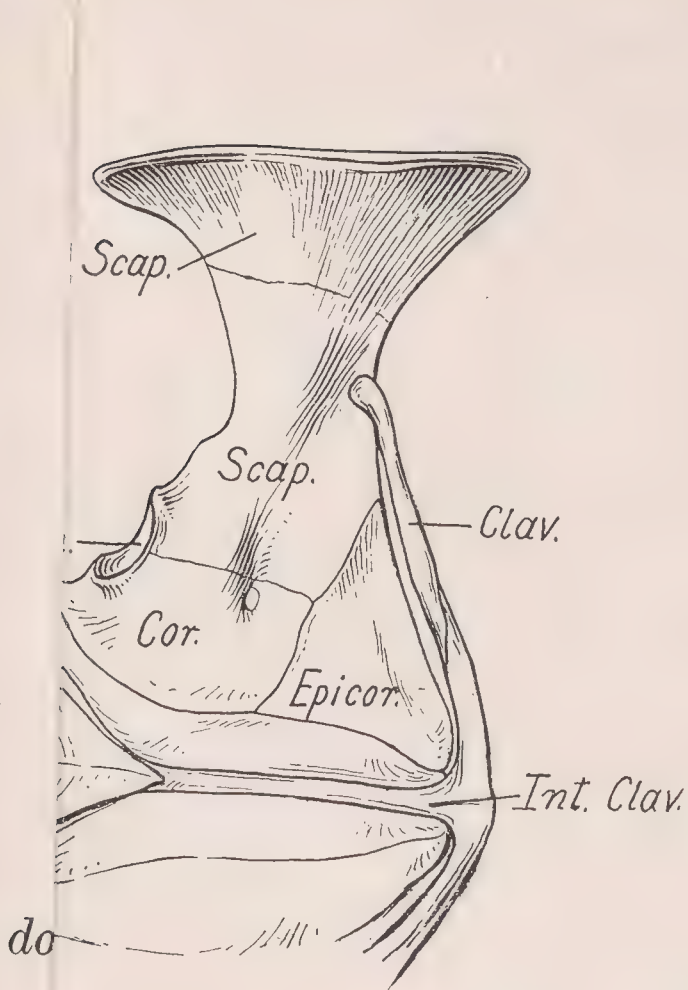
- S*¹*S*² articular surfaces for sacral verterbræ
- longiss. dors* area for longissimus dorsi (including iliocostalis)
- cocc. iliac.* area for coccygeo-iliacus (= m. caudæ dorsalis) + iliocaudalis
- il. tib.* area for iliotibialis (= extensor iliotibialis I Gadow)
- ilio. fem.* area for iliofemoralis
- ilio. fib.* " " iliofibularis
- pub. tib.+ ambiens* " " pubitibialis and ambiens
- obl. abd.* " " obliquus abdominis (on processus lateralis pubis)
- pub. isch. fem. ext.* " " pubi-ischiotrochantericus externus (= p. i. fem. ext. Gadow)
- pub. isch. troch. int.* " " for pubi-ischiotrochantericus internus Osawa (= p. i. femoralis int. Gadow)
- rect. abd.* area for rectus abdominis (on epipubic cartilage)
- isch. troch.* " " ischiotrochantericus Osawa
(= pubi-ischiofemoralis posterior Gadow)
- cocc. isch.* area for coccygeo-ischiadicus (Osawa)
(= ischiocaudalis Gadow)
- isch. tib. post.* area for ischiotibialis posticus Osawa
(= flexor tibialis internus Gadow)
- sph. clo.* area for sphincter cloacæ (Osawa)
(= Aftermuskeln *α*, *β*, *γ*, etc. Gadow)

B.—*Ornithorhynchus*. General location of the chief muscle areas of the pelvis: Oblique view from the right side and partly from below. Data chiefly from Coues.

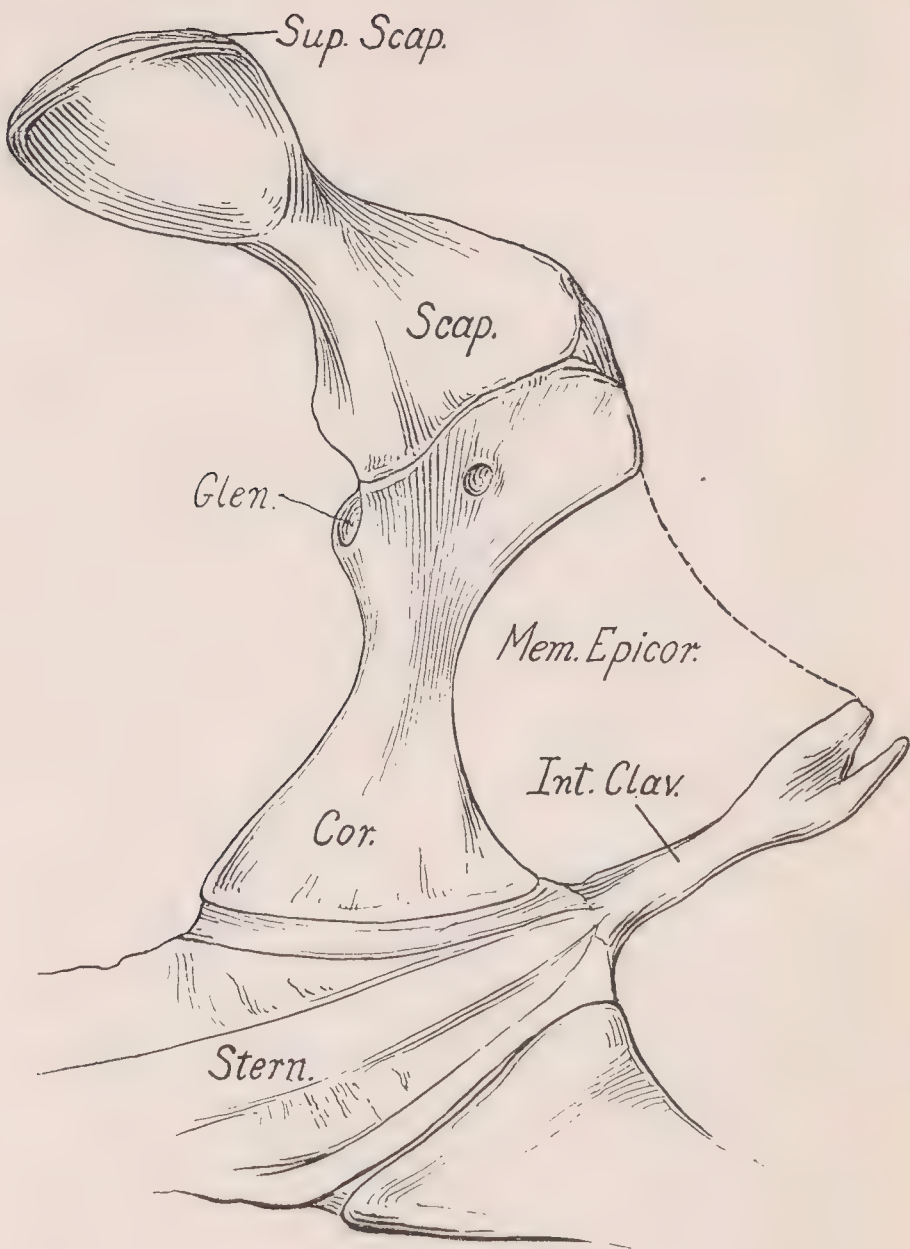
- glut. min., glut. med.* areas for the deep gluteal muscles (derived from iliofemoralis)
- iliacus, pectineus, ps. min.* } areas for the iliacus pectineus and psoas
minor muscles which collectively represent the pubi-ischiofemoralis internus.
The psoas minor is attached to the "pectineal process" along with the sartorius.
- add. brev.* area for adductor brevis (= ?longus)
- add. long. add. mag.* adductor longus, magnus
The adductor series probably represents the more peripheral parts of the pubi-ischiofemoralis externus of *Sphenodon*, while the obturator externus represents the more central part.
- pyram.* area for pyramidalis abdominis
- rect. fem.* " " rectus femoris (probably derived from ambiens)
- quad. fem.* " " quadratus femoris (probably derived from pubi-ischiofemoralis posterior, along with obturator internus and gemellus inferior)
- semitend.* area for semitendinosus (probably derived from flexor tibialis externus)
- biceps* " " biceps (probably derived from iliofibularis)
- semimemb.* " " semimembranosus, derived from flexor tibialis internus (ischio-tibialis)

C.—*Cynognathus*. Inferred location of muscle areas. Abbreviations as in preceding figures.

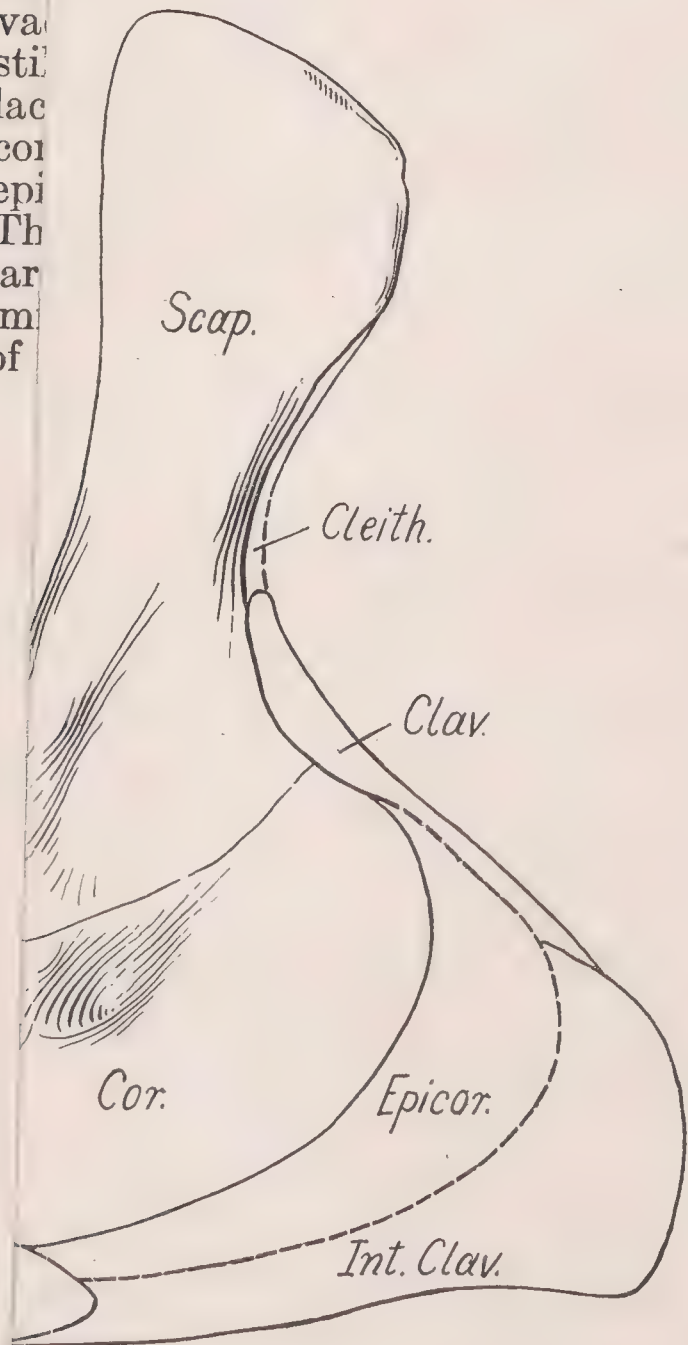




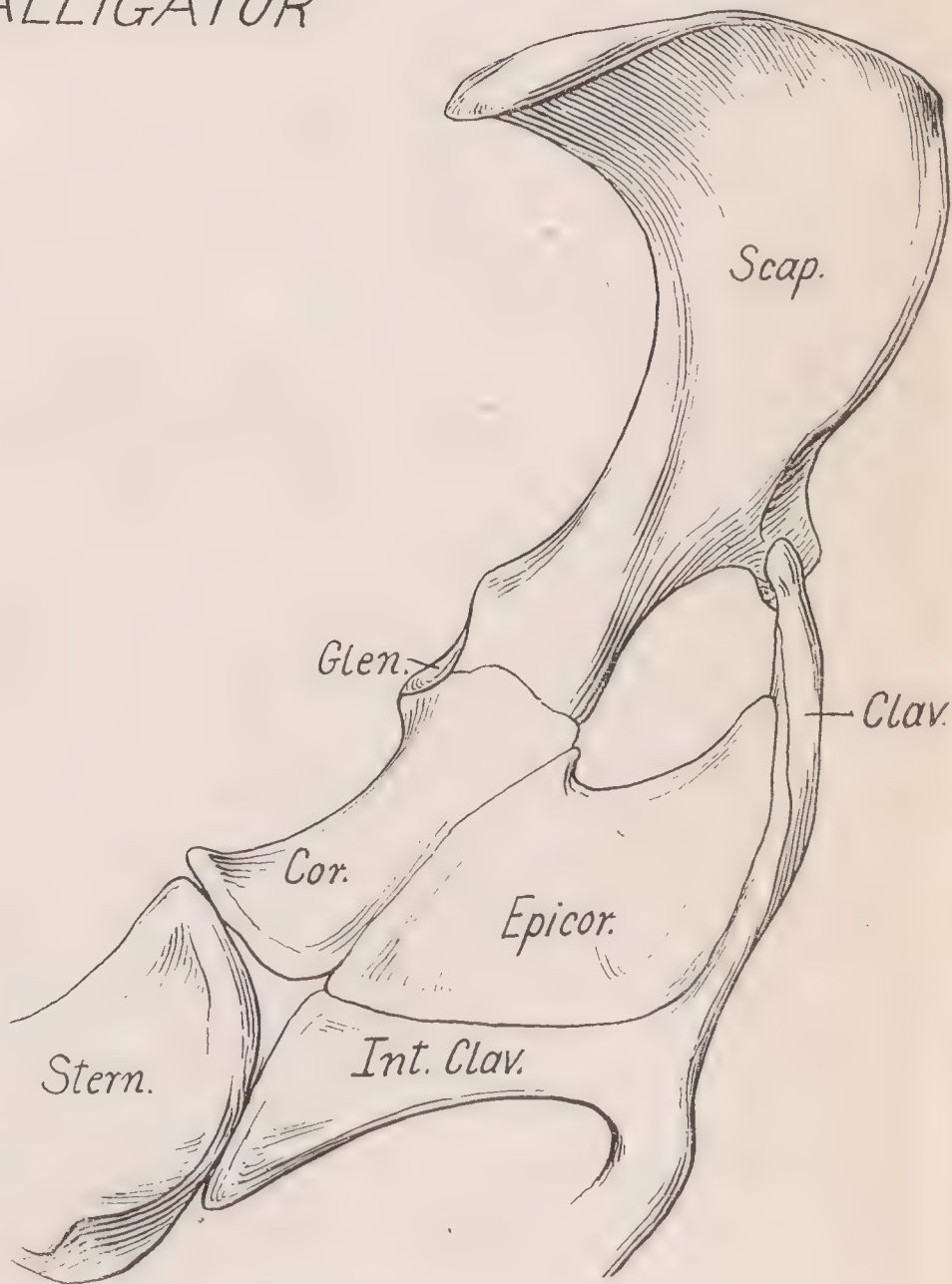
MOSCHOPS



ALLIGATOR



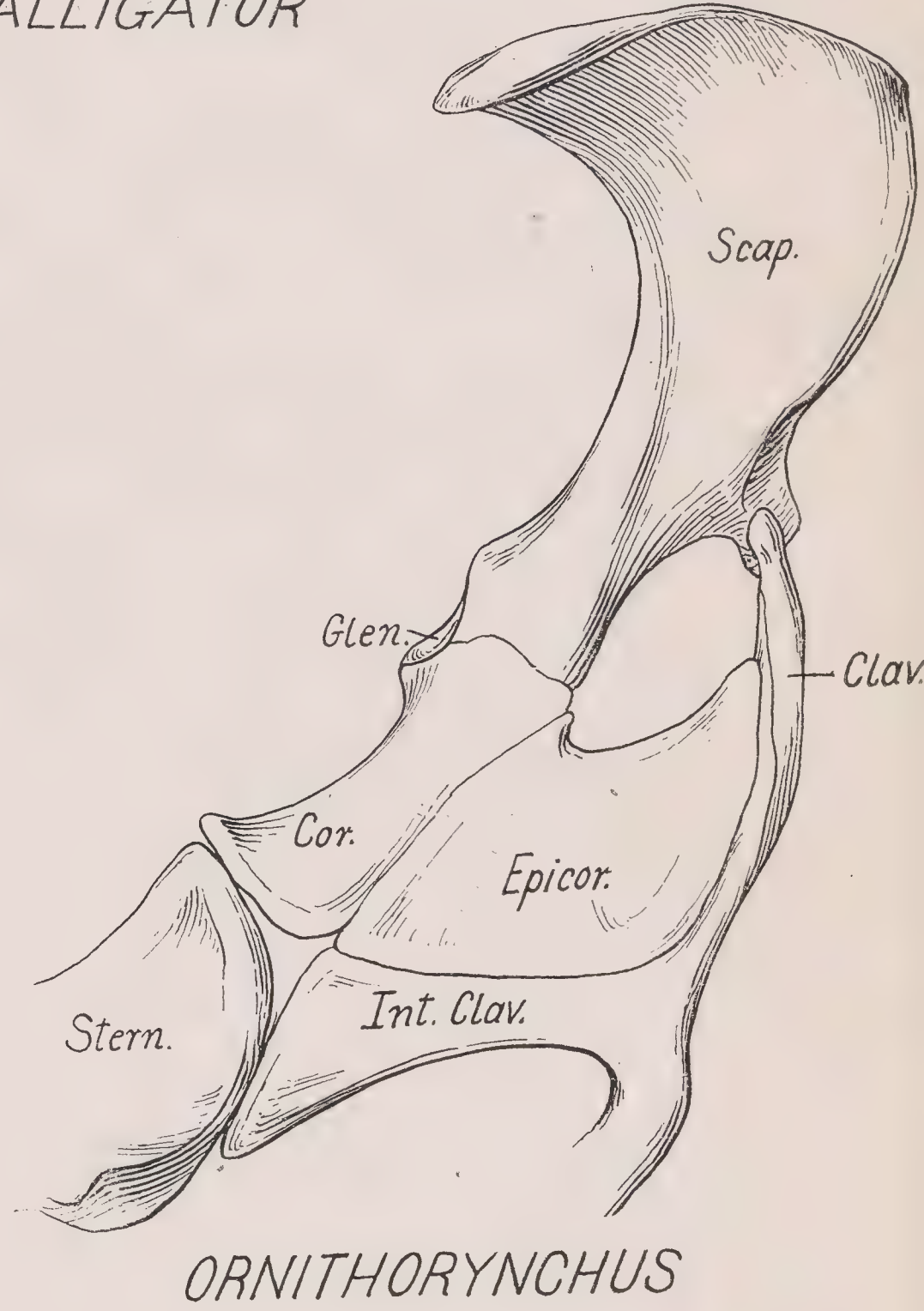
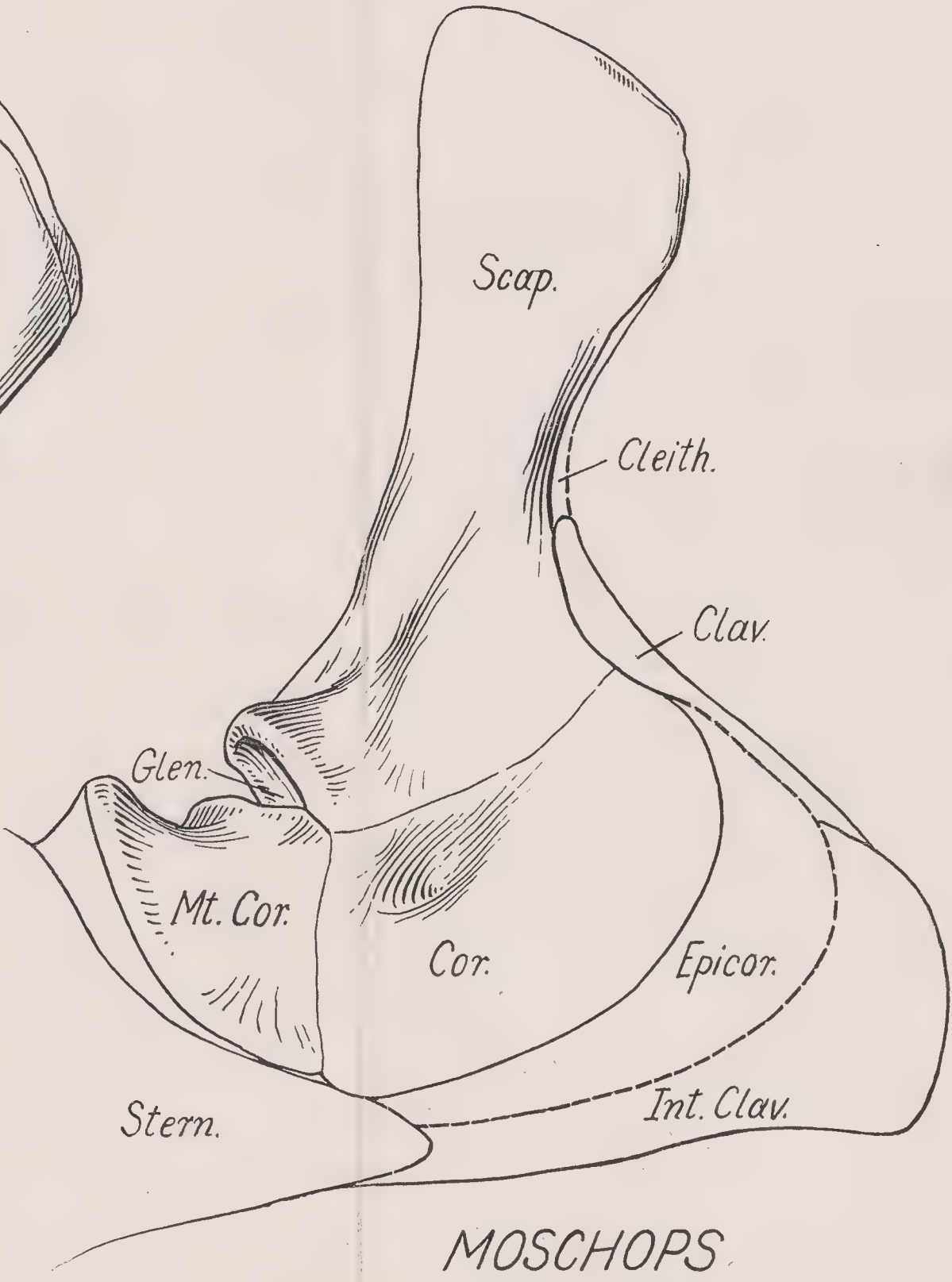
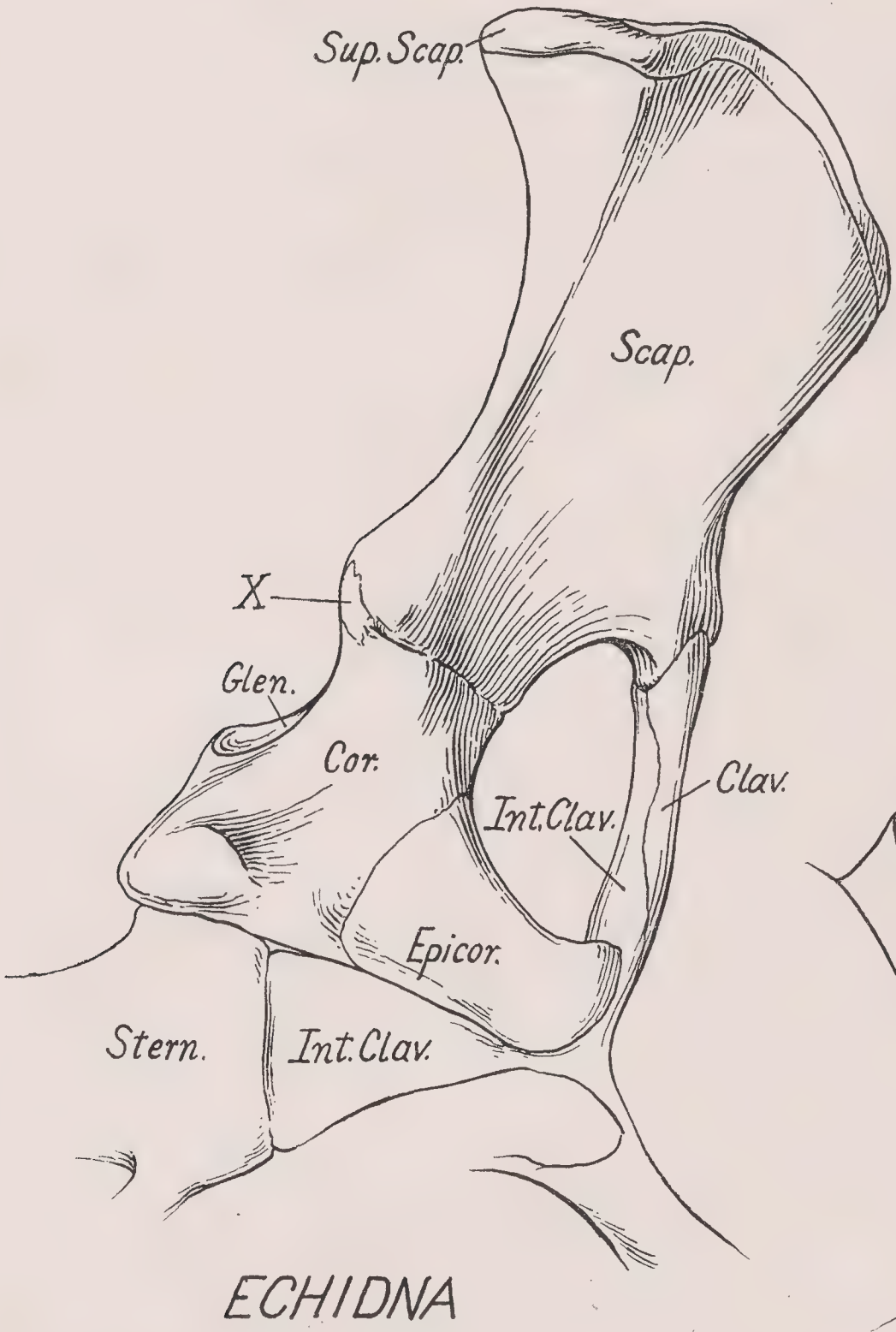
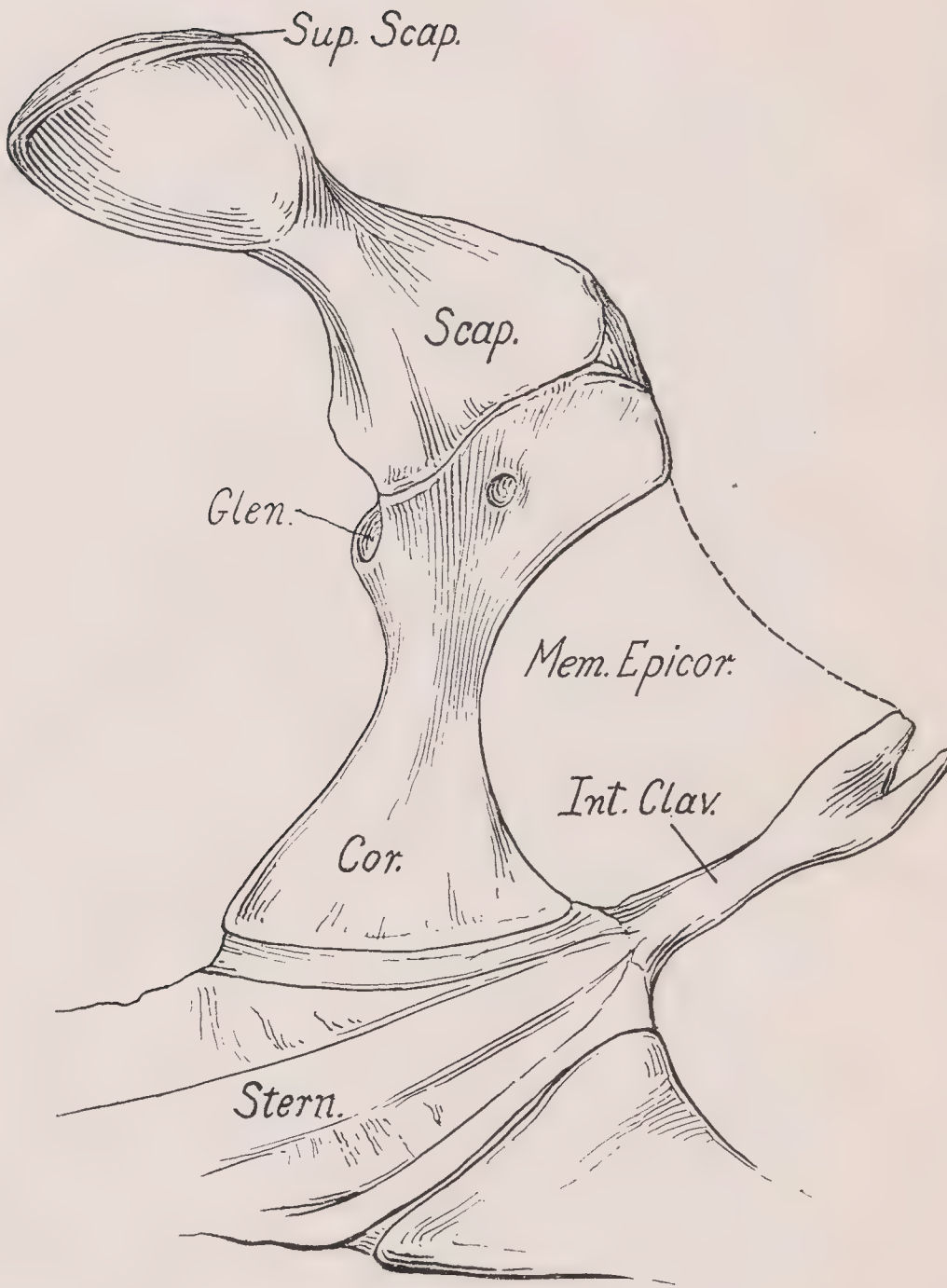
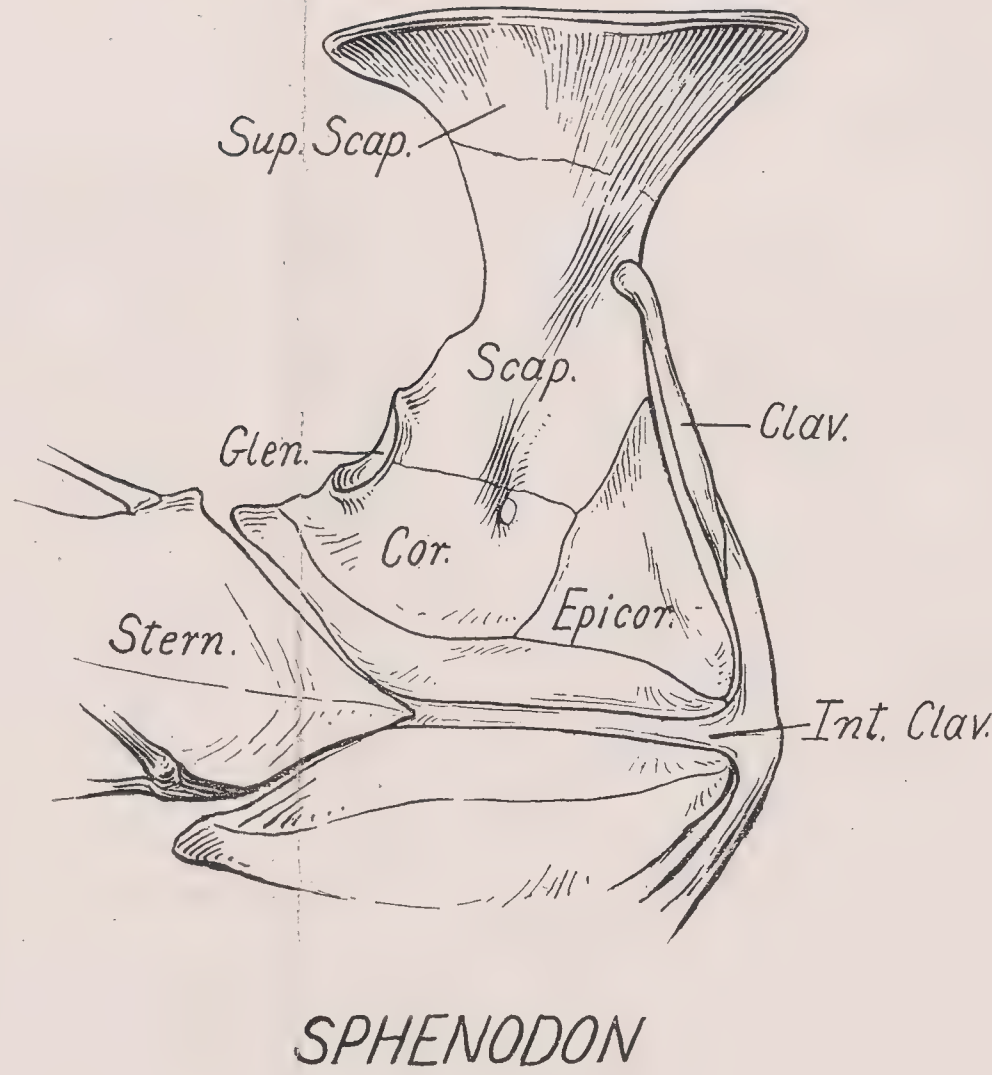
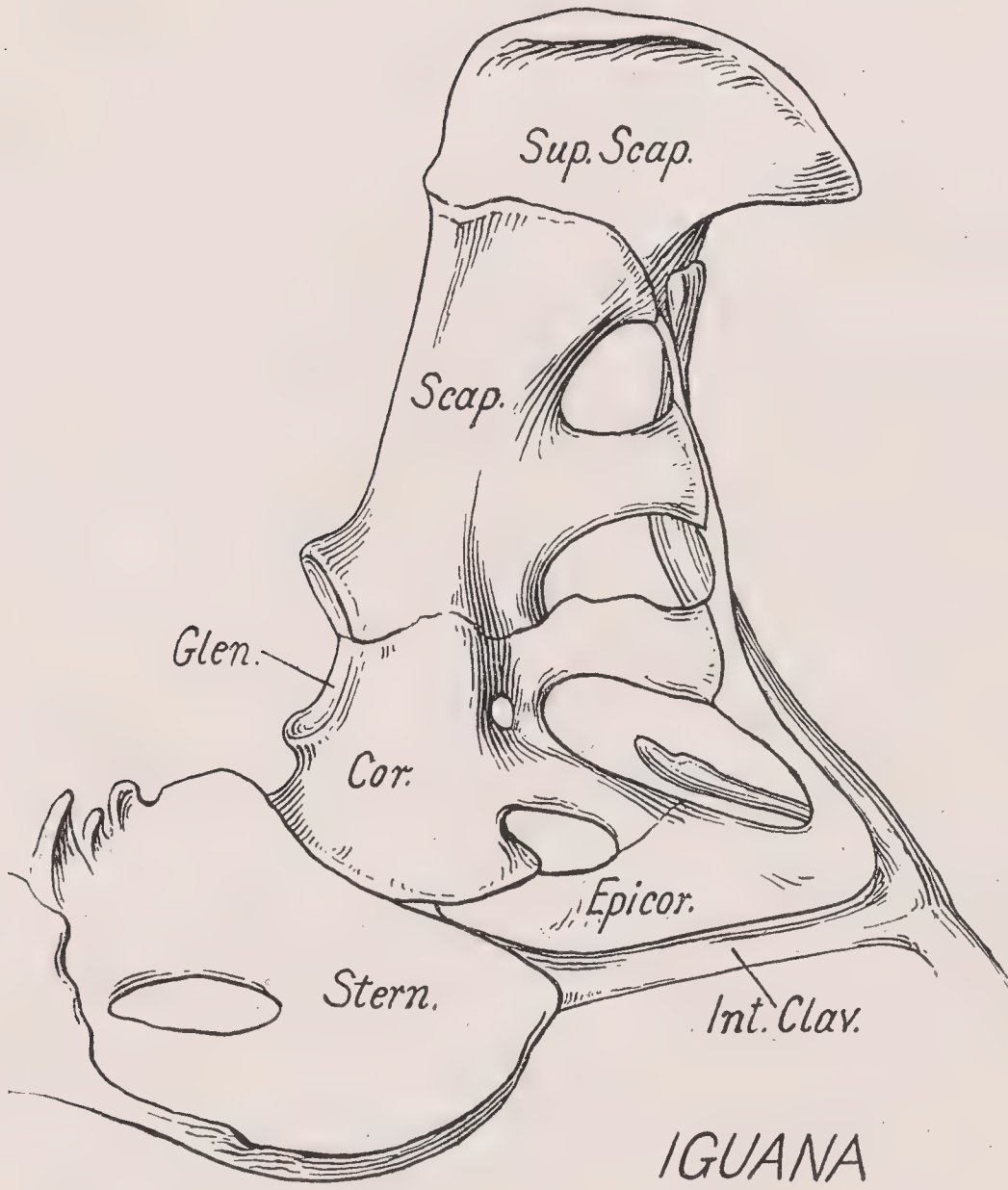
MOSCHOPS



ORNITHORYNCHUS

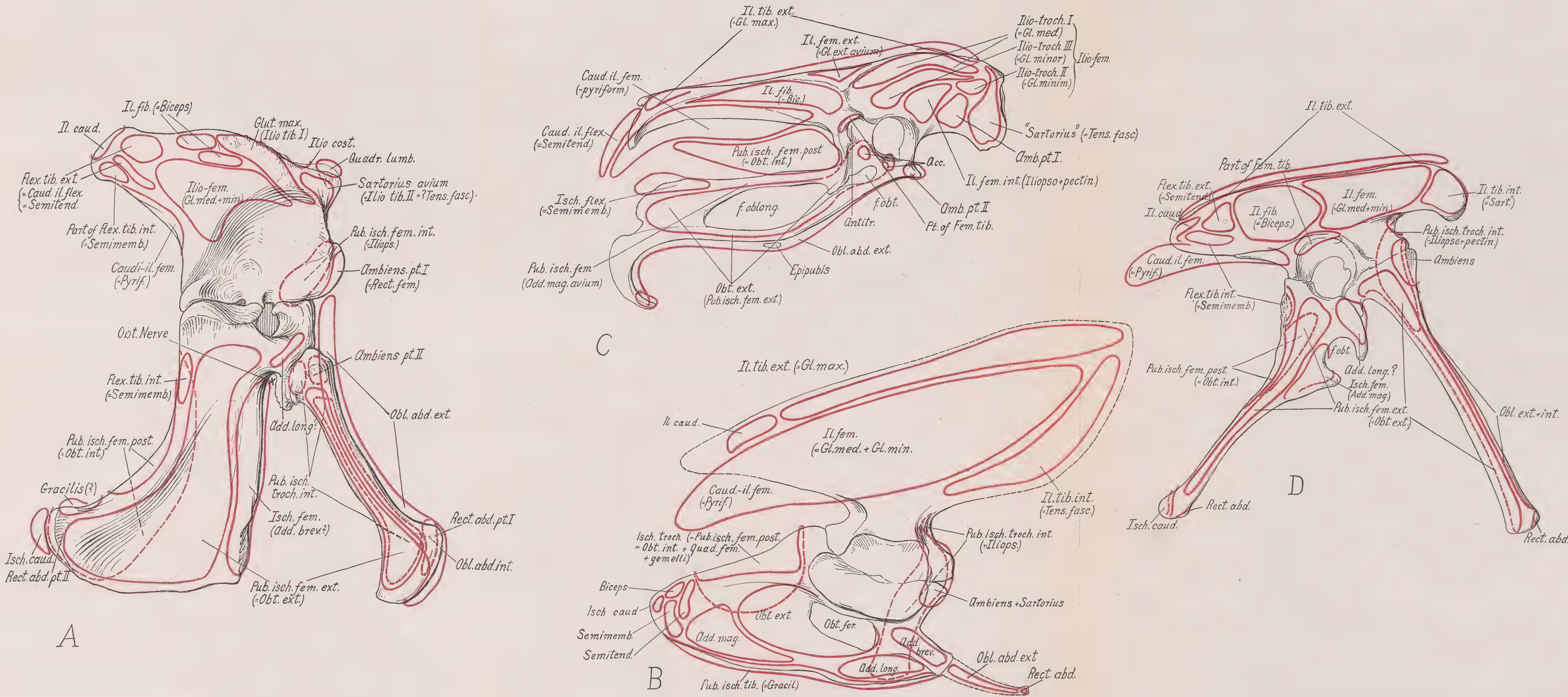
Inner surface of the left half of the pectoral girdle of *Iguana*, *Sphenodon*, *Alligator*, *Echidna*, *Moschops* and *Ornithorhynchus*.

The most primitive conditions in the series are seen in the Permian reptile *Moschops*, which retains all the original elements including the cleithrum and the metacoracoid. The presence of a membraneous epicoracoid is indicated by the form and relations of the coracoid in the mounted specimen. *Sphenodon* has lost the cleithrum and the metacoracoid but is otherwise primitive. In *Iguana* secondary vacuities are developed in the coracoid and scapula. In *Alligator* the single coracoid, still pierced by the supracoracoid foramen, is extended transversely; the clavicle is lacking but the epicoracoid is probably represented by the membrana episterno-coracoideus. In *Echidna* and *Ornithorhynchus* the metacoracoid is lost and the epicoracoid, perhaps in adaptation to fossorial habits, becomes thick and well ossified. The coracoid is not perforated by the supracoracoid nerve, which passes through the large secondary opening above the epicoracoid. A vestigial ossicle (X) in a certain immature specimen of *Echidna* has somewhat the position of the metacoracoid but is of very doubtful homology.



General location of the principal muscle areas of the pelvis.
A.—Alligator, data chiefly from Gadow.
B.—Cynognathus, tentative location of areas.
C.—Struthio, data chiefly from Gadow. (Compare text figure 10).
D.—Ornitholestes, tentative location of areas. (Compare text figure 10).

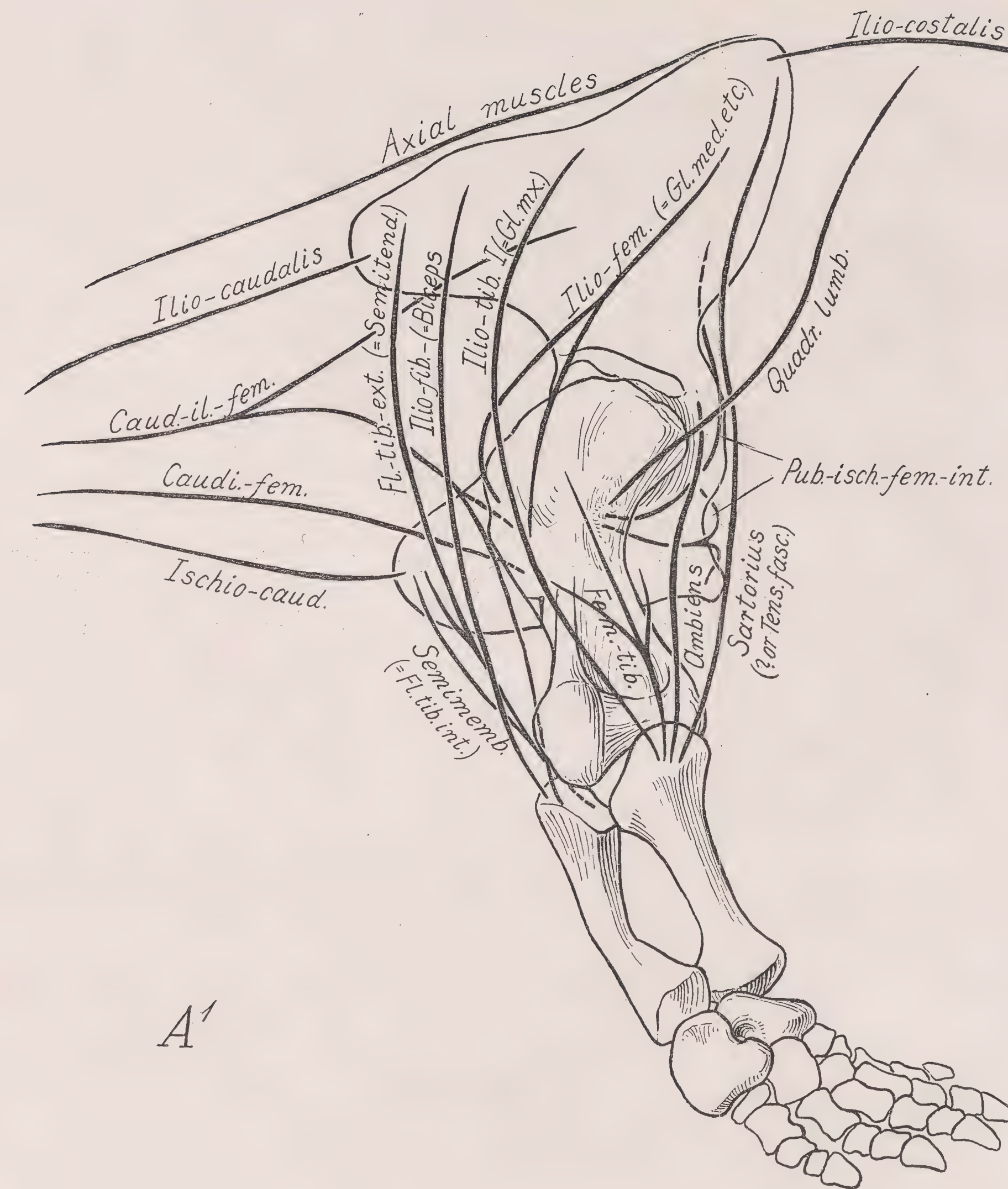
The homology of the true adductor series of *Cynognathus* and mammals with the so-called adductors of birds seems doubtful. The adductors of mammals are more peripheral in position lying external to the obturator externus and derived at least in part from the ischiofemorals of reptiles. The "adductor magnus" of birds on the contrary arises dorsad to the obturator externus and is beneath the obturator internus.



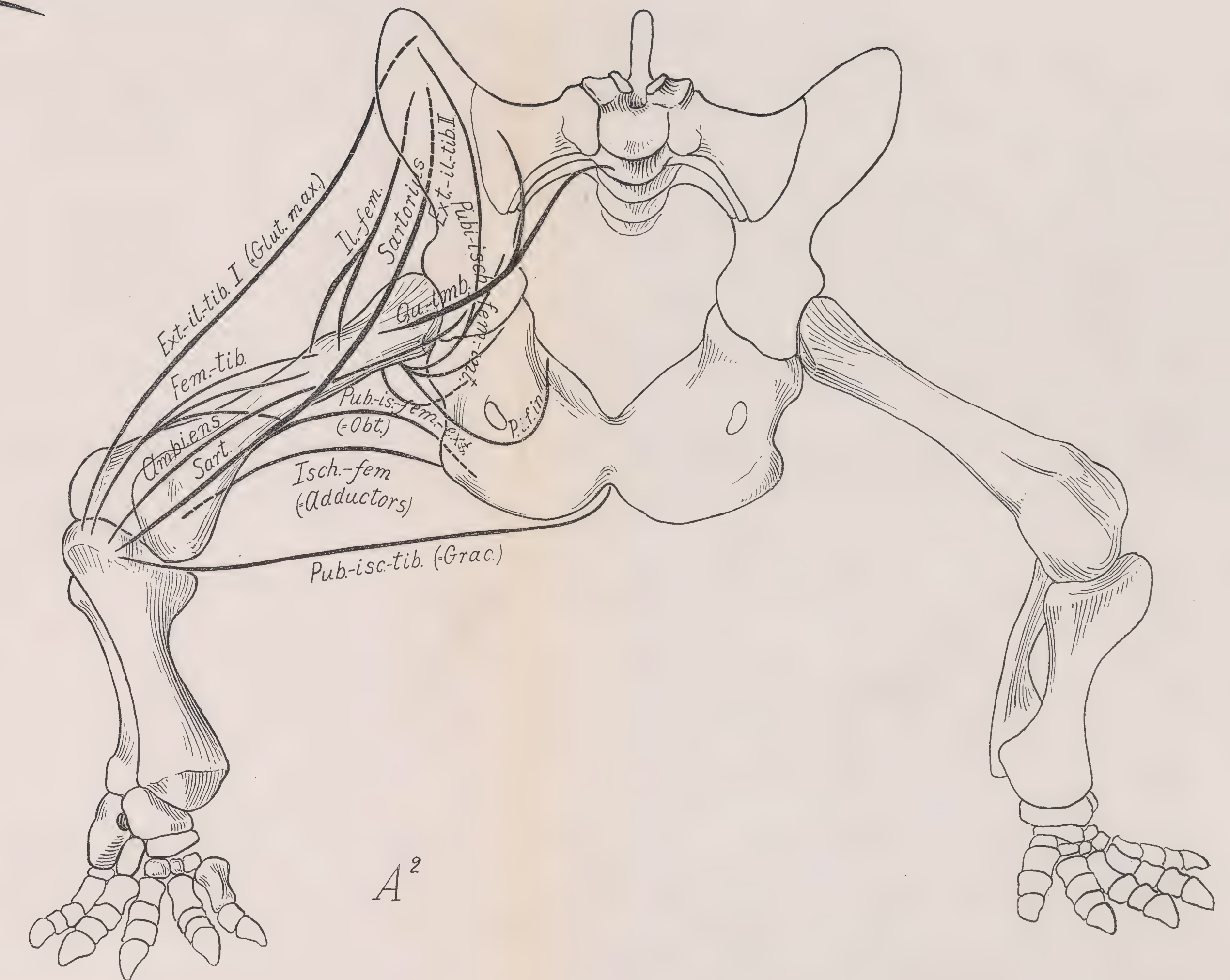
Moschops capensis Broom. Mounted pelvis and hind limbs (A. M. N. H.), $\times \frac{2}{3}$, with tentative general location and direction of the principal pelvic muscles.

A¹.—Right side, lateral aspect.

A².—Front view, showing left limb directed outward and backward, right limb outward and forward.



A¹

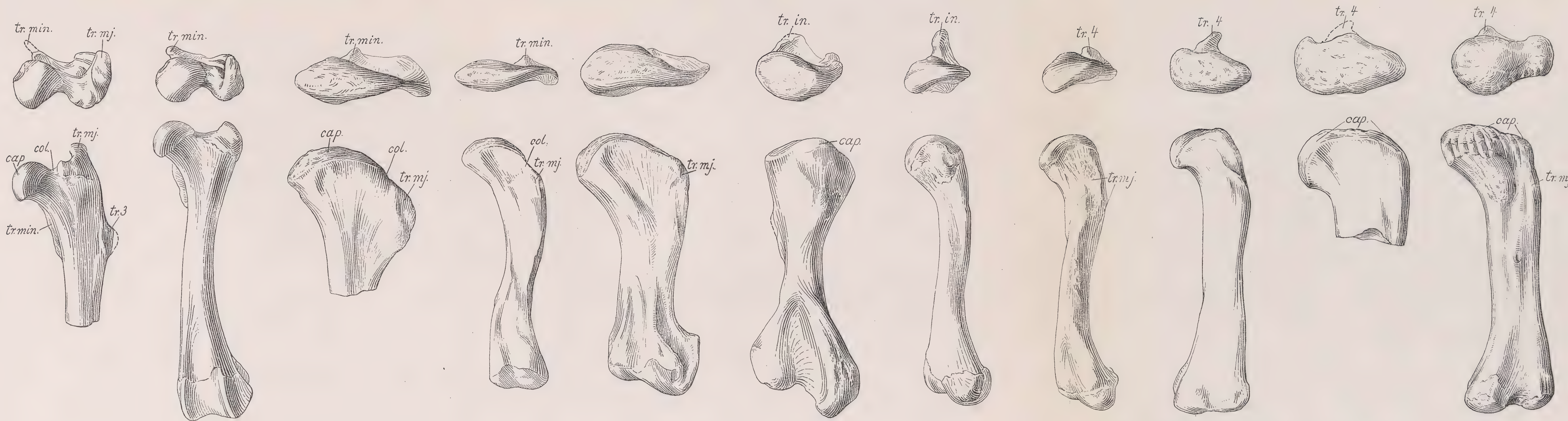


A²

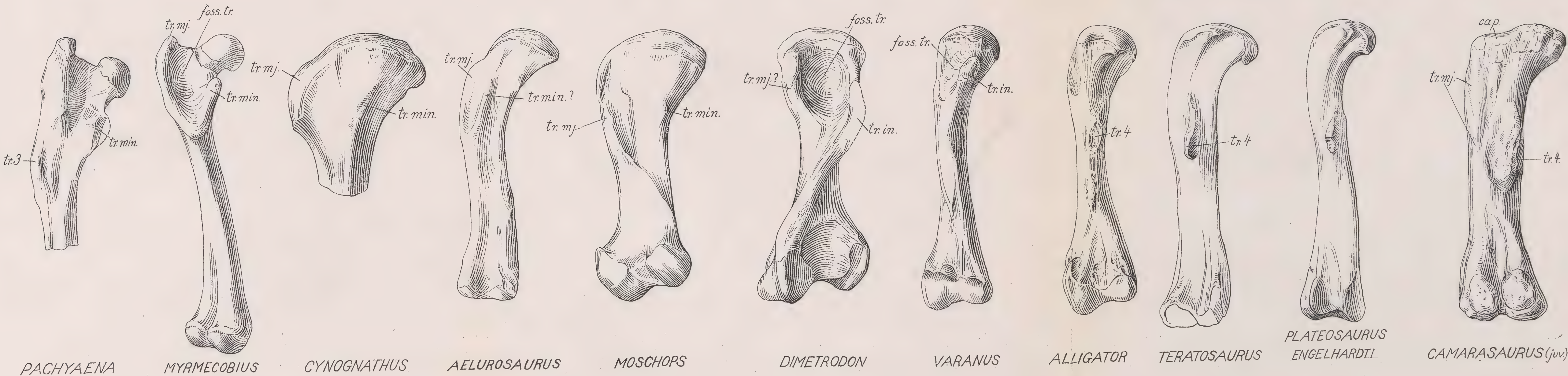
A series of femora of reptiles and mammals illustrating the morphology of the femoral trochanters. Scales various.
Upper row, proximal view.
Middle row, front (anterosuperior) view.
Lower row, back (posteroinferior) view.

- cap. caput femoris
- tr. min. trochanter minor (lesser trochanter), homologous with
- tr. in. trochanter internus, homologous with
- tr. 4 trochanter quartus
- tr. mj. trochanter major (great trochanter)
- col. collum femoris
- tr. 3 trochanter tertius
- foss. tr. fossa trochanterica

The most ancient and primitive type is in the center (*Dimetrodon gigas*). This has a deep trochanteric fossa and a high internal trochanteric, or adductor, crest, which probably served for the attachment of the ischiofemoralis (adductors), pubi-ischiofemoralis externus (obturator externus) and pubi-ischiofemoralis internus (iliopsoas + pectineus). At the left of the primitive type is the Therapsid-Mammal series, culminating in the marsupial (*Myrmecobius*) and primitive placental (*Pachyaena*) types, in which the internal trochanteric crest gives rise to the lesser trochanter (for the iliopsoas + pectineus). On the right of *Dimetrodon* is a morphological series leading toward the dinosaurs and showing the derivation of the fourth trochanter (for the insertion of the ischiofemoralis and caudifemoralis) from the internal trochanteric crest.



GRESSLYOSAURUS



PACHYAENA

MYRMECOBIUS

CYNOGNATHUS

AELUROSaurus

MOSCHOPS

DIMETRODON

VARANUS

ALLIGATOR

TERATOSAURUS

PLATEOSAURUS
ENGELHARDTII

CAMARASaurus (juv)

Hum. Ant.

a Cor.

*Cor. Hum.
ch. Brev.)*

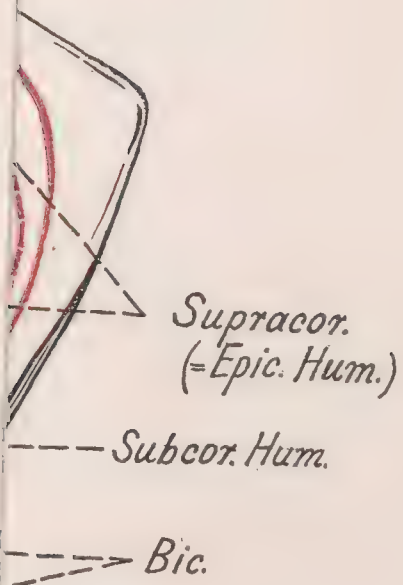
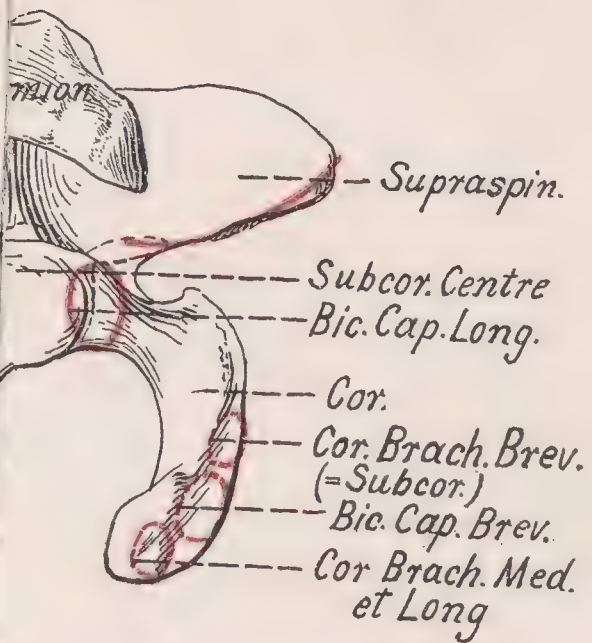
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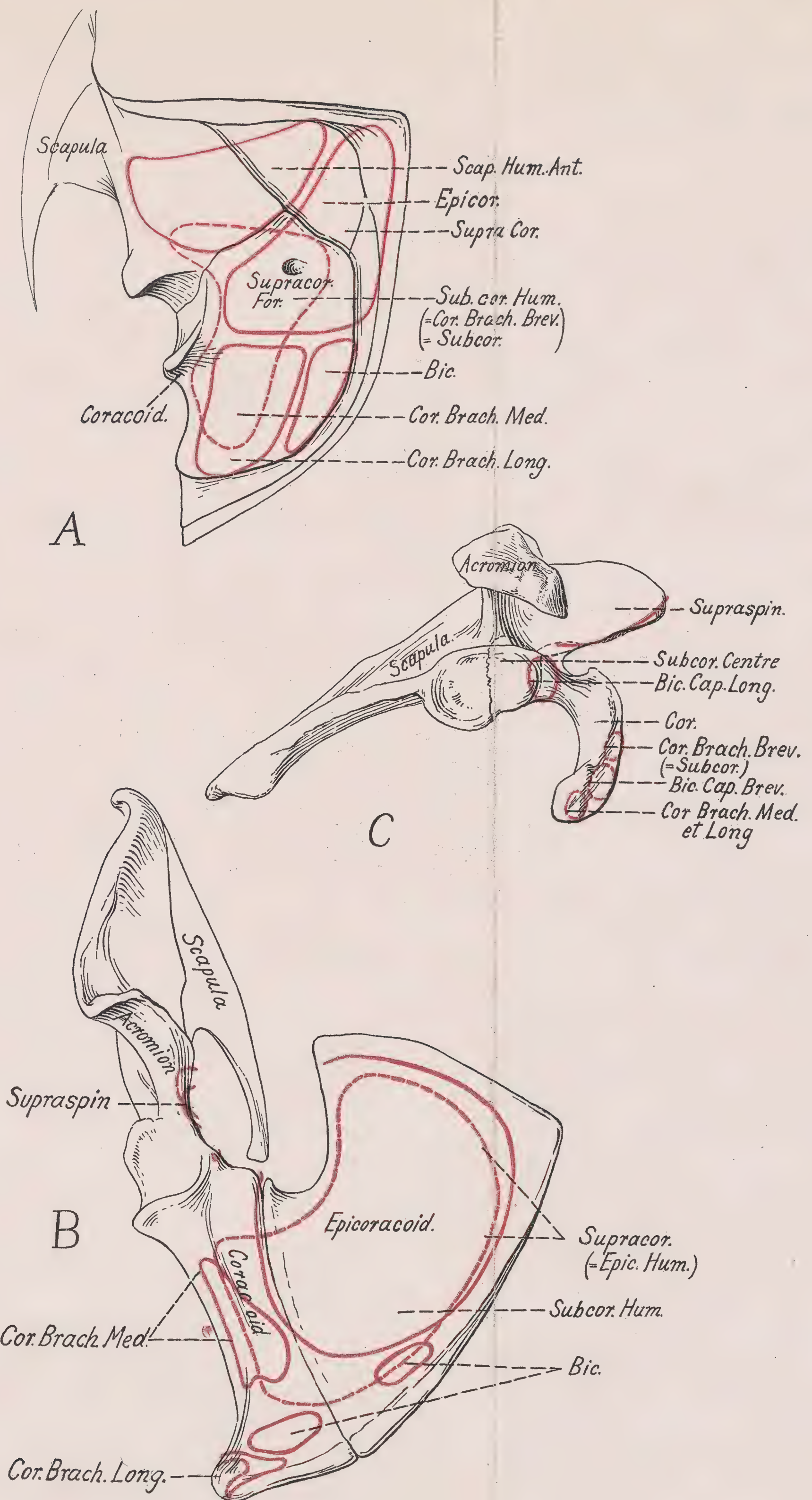
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Ventral view of the coracoid region of (A) *Sphenodon*, (B) *Ornithorhynchus*, (C) *Homo*, showing the location of the principal muscle areas.

In all three cases the true coracoids serve for the origin of the coracobrachialis medius, the c. b. longus and the biceps muscles, while from the epicoracoids of *Sphenodon* and *Ornithorhynchus* arise the subcoraco-humeralis (= coracobrachialis brevis) and the supracoracoideus muscles. The "subcoracoid" centre of mammals is probably a new structure associated with the intracapsular origin of the long head of the biceps.

The supraspinatus muscle of mammals may have been derived either from the scapulohumeralis anterior or from the supracoracoideus of primitive reptiles.



anterior and posterior basal cusps. Canines large, incisors quite small, as in Creodonta.

The submedian position of *pa* and *me* in the upper molars, and simple and high premolars easily distinguish this genus. The lower molars have been confused with *Palæosinopa* and *Diacodon*. From the former they are distinguished by narrower heel, higher trigonid with *pr*^d overtopping *pa*^d and *me*^d; from the latter by greater breadth of trigonid, lower *me*^d and higher *pa*^d.

The position of this genus is very doubtful. Cope¹ referred it to the Creodonta, and to the family Leptictidæ in the vicinity of *Deltatherium*, to which genus he had at first referred it. The molars differ considerably in construction from *Deltatherium*, and the premolars hardly less so. The broad outer shelves of the upper molars, transverse *m*³, and shearing trigonids of the lower molars are suggestive of *Sinopa*. On the other hand,

A.M. 4228 Type

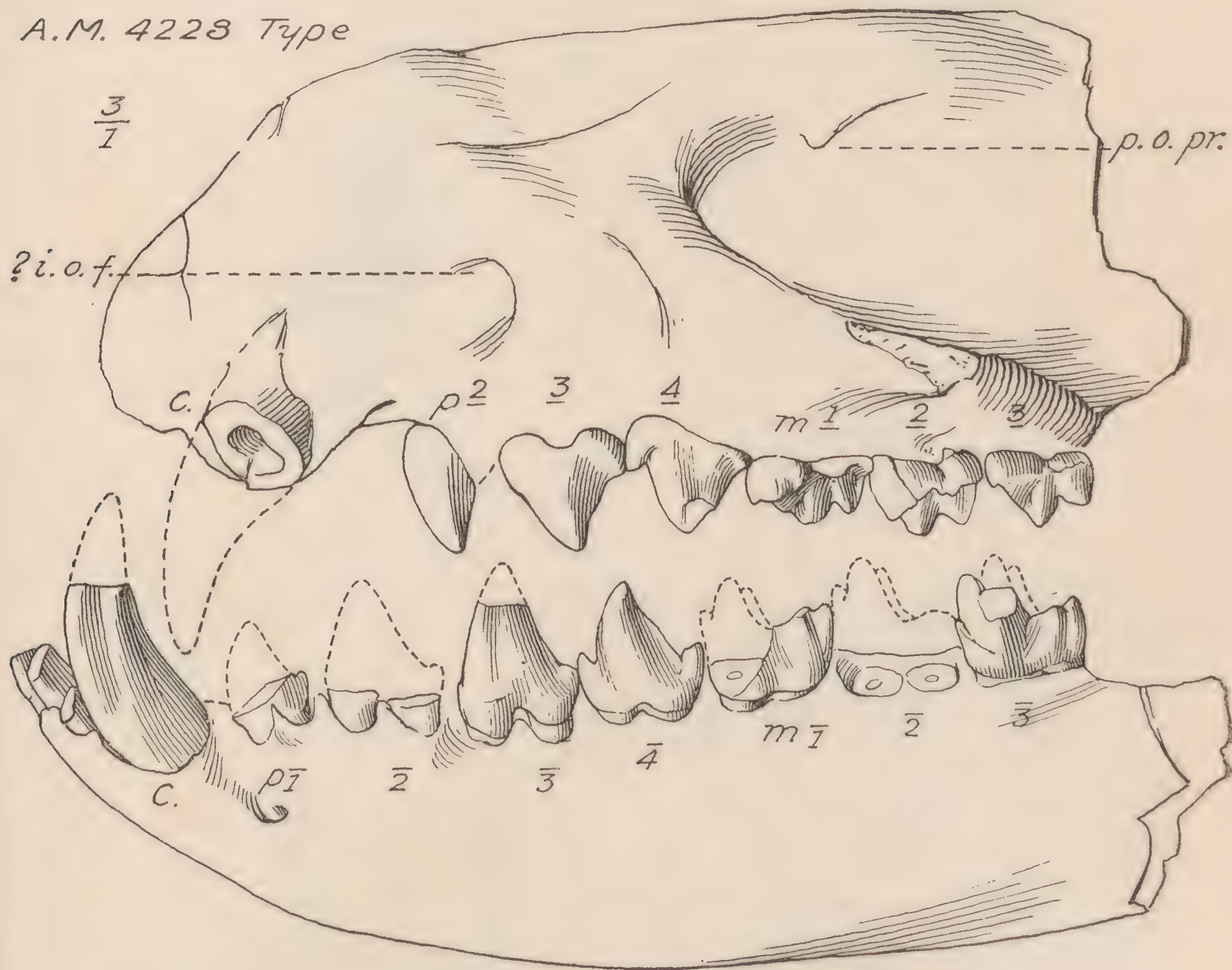


Fig. 10. *Didelphodus absarokæ*. Front of skull and lower jaw, type specimen, side view, three times natural size. Lower Eocene, Wasatch, Bighorn basin, Wyoming. Probably from the lower part of the formation, Gray Bull or Sand Coulée horizon. Cope Coll., Amer. Mus. No. 4228, collected by J. L. Wortman in 1881. *I. o. f.*, infraorbital foramen; *p. o. pr.*, postorbital process.

¹ Cope, 1885, Tertiary Vertebrata, Rep. U. S. Geol. Surv. Terrs. (Hayden), III, p. 283.

the teeth are in many respects not unlike those of the Leptictidæ, except that in the typical leptictids p_4^4 are more complex, submolariform, the broad outer shelf of the upper molars and other shearing specializations are lacking. The basicranial region of the skull and the skeleton would probably afford diagnostic characters, but these are unknown or at least have not been correlated with the teeth.

The problematic Bridger genus *Phenacops* appears to be an ally of *Didelphodus*, and for the present both may be referred provisionally to the Leptictidæ, although not nearly related to the typical members of that family.

Except for a superficial resemblance in the molars to certain Didelphidæ there is nothing in the teeth, skull or jaws to suggest marsupial affinities.

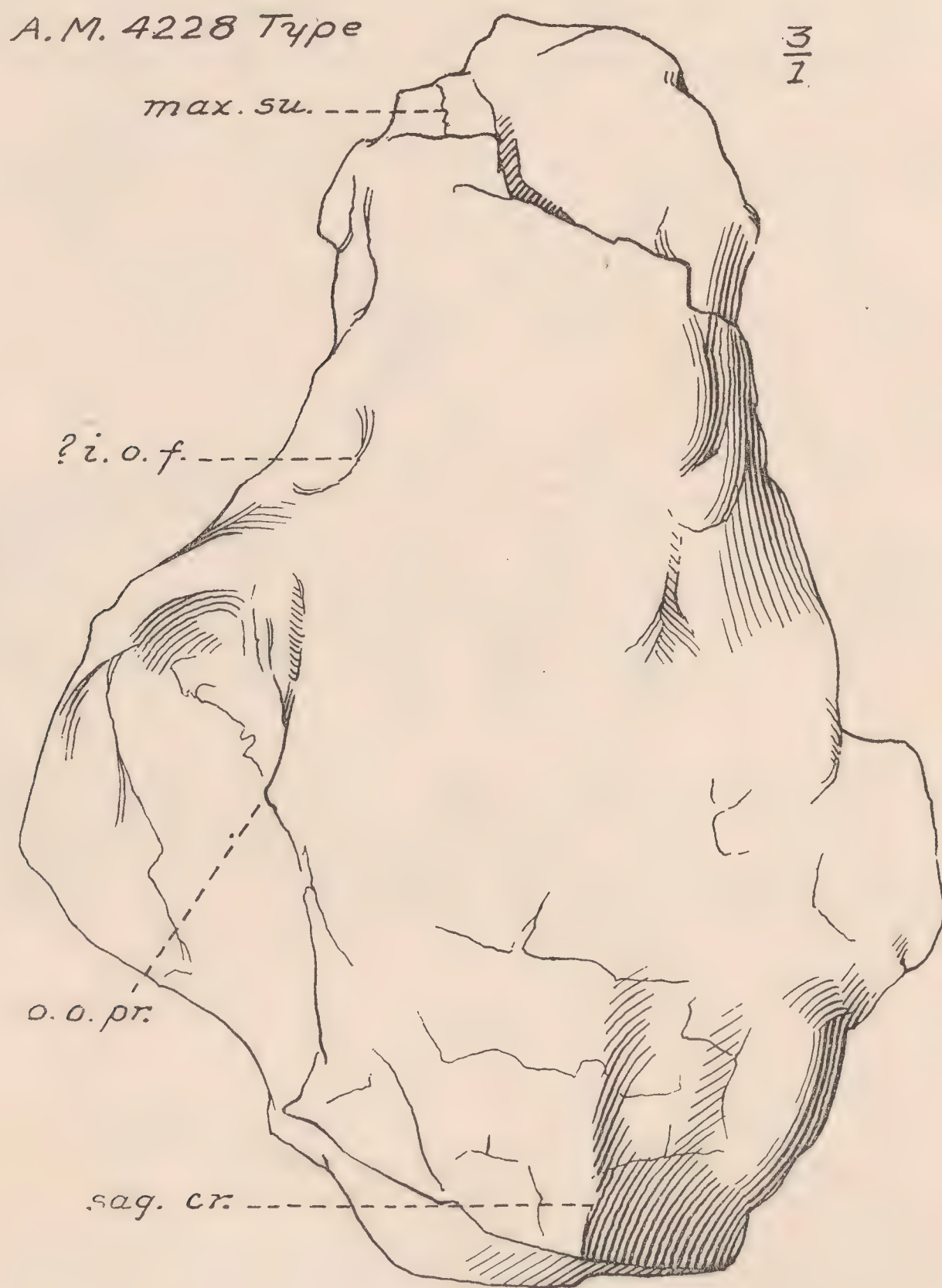


Fig. 11. *Didelphodus absarokæ*. Superior view of type skull, three times natural size. *I. o. f.*, infraorbital foramen; *max. su.*, suture between maxilla and premaxilla; *sag. cr.*, anterior end of sagittal crest.

A.M. 4228 Type

$\frac{3}{1}$

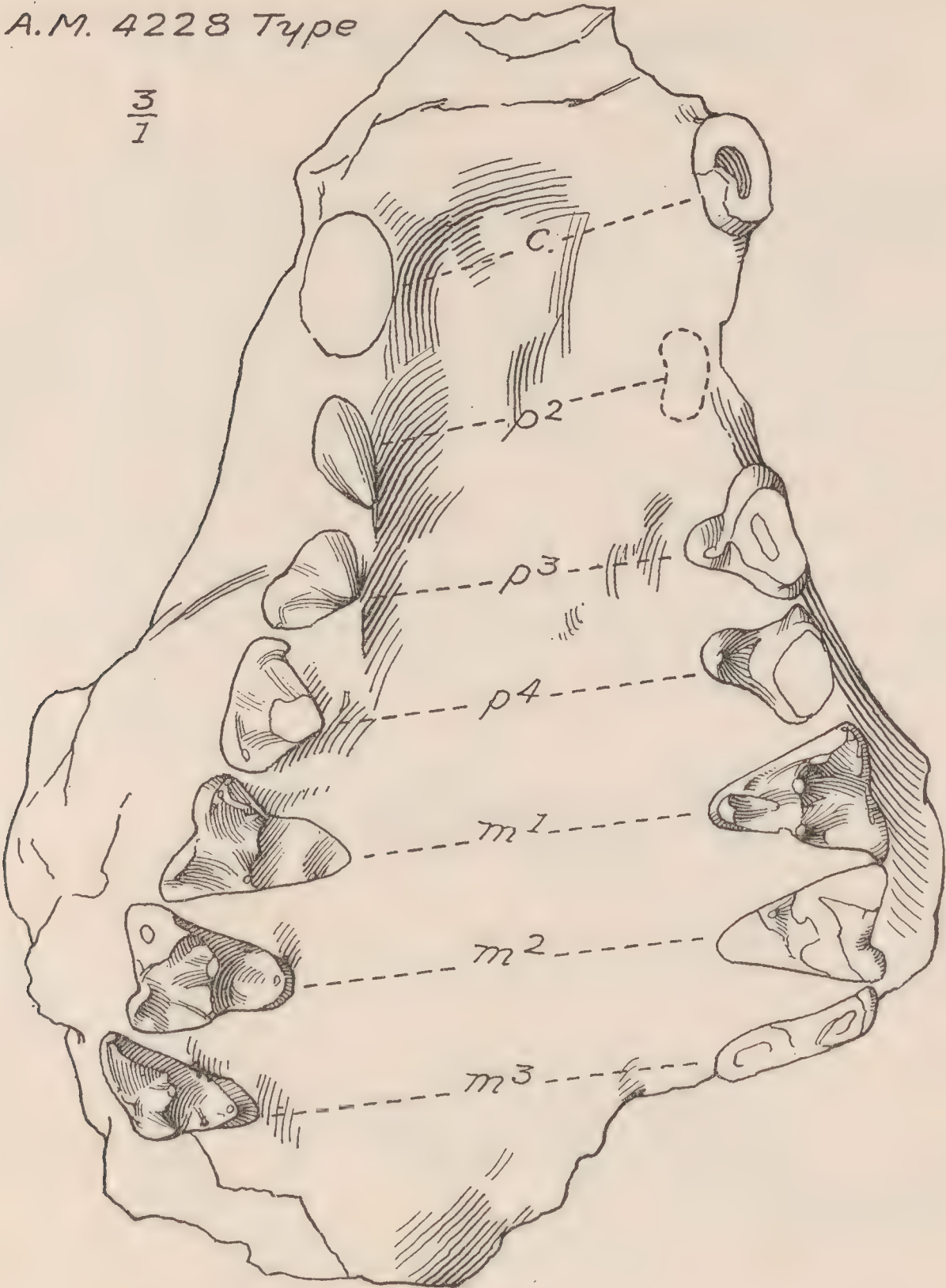


Fig. 12.

A.M. 4228 Type

$\frac{3}{1}$

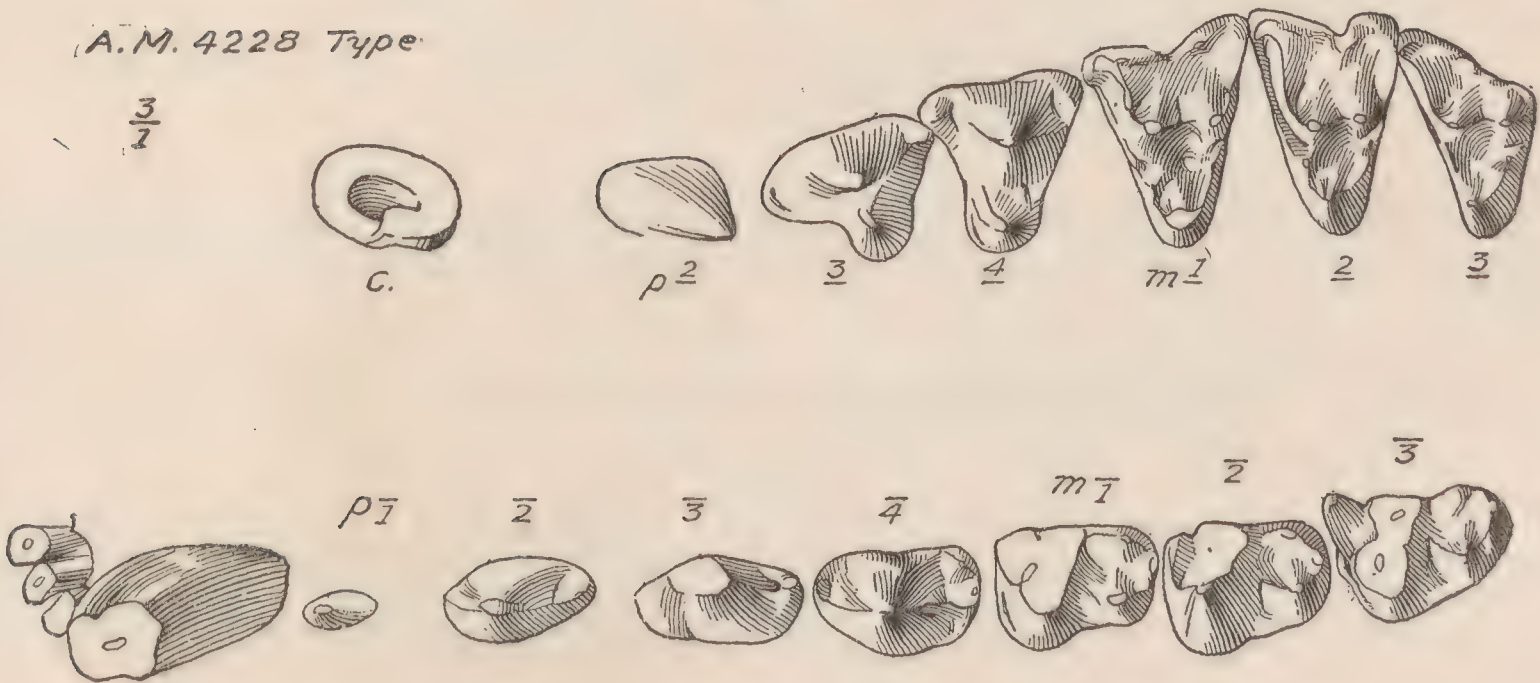


Fig. 13.

Fig. 12. *Didelphodus absarokæ*. Palatal view of type skull, three times natural size.
Fig. 13. *Didelphodus absarokæ*. Crown views of upper and lower teeth, three times natural size.
From the type, supplemented by Nos. 15770, 16238.

Didelphodus absarokæ (Cope, 1881)

Figs. 10-13

Specific characters.— $I_1^1-m_3 = 32$ mm.; $m_{1-3} = 11$; $p_{1-4} = 15.3$. First lower premolar set obliquely. There is but one species at present known so that the specific and generic characters are not separable.

The *type*, Amer. Mus. No. 4228, consists of the anterior half of a skull and the lower jaws, partly buried in hard matrix and with the teeth much damaged. No. 4229, part of a lower jaw with three well preserved molars. No. 15700, part of upper jaw with m^{1-3} ; No. 15101, lower jaw, $m_{1-2r.}$; and No. 15102, part of lower jaw with m_{1-3} , all from the Bighorn Wasatch. No. 16238, lower jaws, from the New Mexican Wasatch (lower beds) agrees with the type except in the reduction of m^3 , but I have some doubts about its reference to the same species.

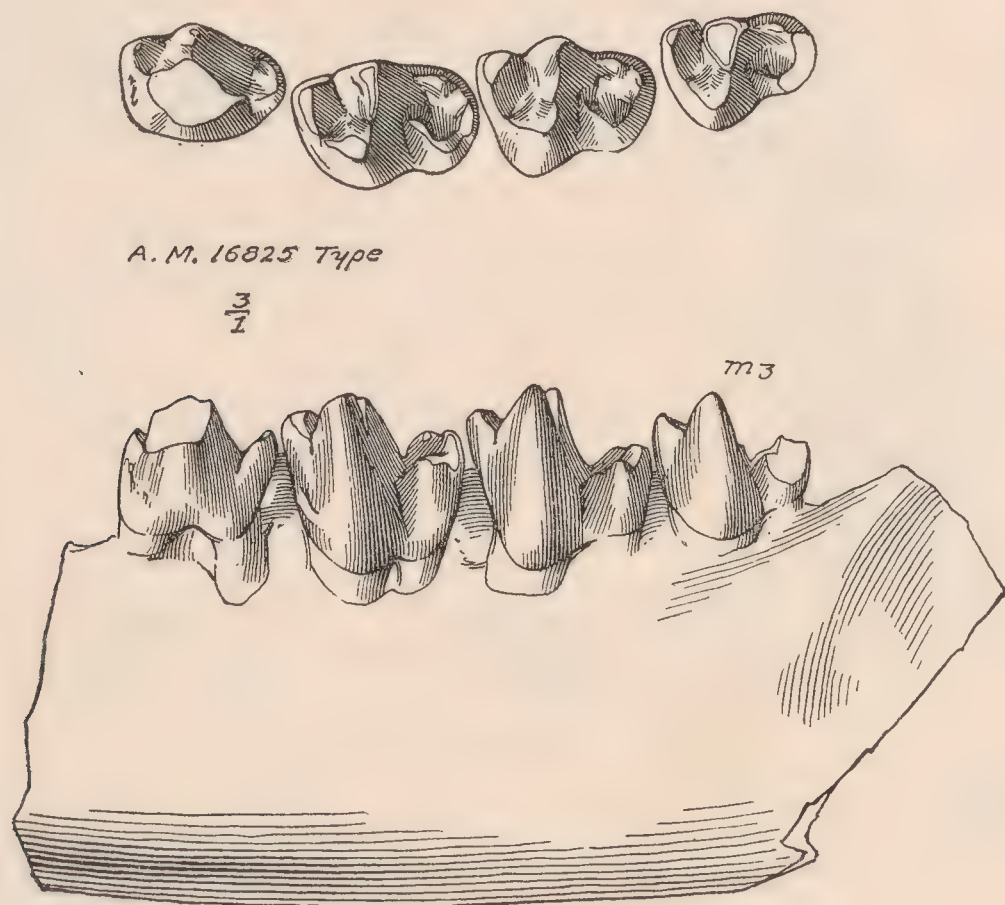


Fig. 14. *Didelphodus absarokæ secundus*. Type specimen, lower jaw, external view, with crown view of teeth, three times natural size. Upper Gray Bull beds of Wasatch formation, Bighorn basin, Wyoming.

Didelphodus absarokæ secundus, new mutation

Fig. 14

Type.—Amer. Mus. No. 16825; part of lower jaw with p_4-m_3 ; from upper level of Gray Bull beds, at head of Ten-mile Creek in the Bighorn Basin.

Distinctive characters.— P_4 more robust than in *D. absarokæ*, the anterior basal and internal cusps stronger. M_3 more reduced.

***Didelphodus absarokæ ventanus*, new mutation**

Fig. 15

Type.— Amer. Mus. No. 14747; right ramus of jaws with p_3 and heels of m_{2-3} and roots of remaining postcanine teeth. Lost Cabin beds of Alkali Creek, Wind River Basin.

Distinctive characters.—Teeth somewhat smaller and narrower; p_3 with anterior basal cusp and heel and rudimentary inner cusp; m_3 smaller in proportion than in the preceding types.

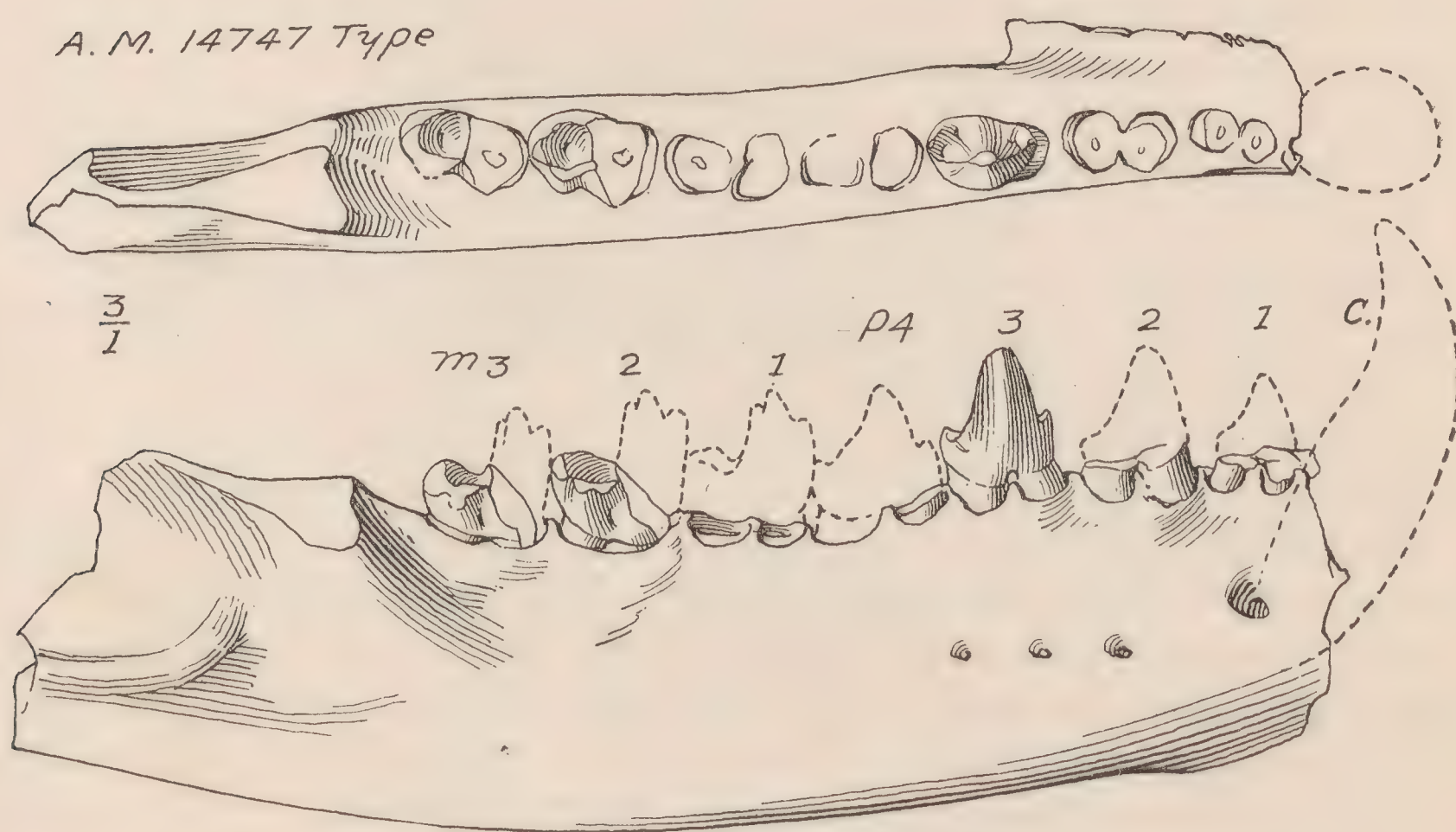


Fig. 15. *Didelphodus absarokæ ventanus*. Type specimen, lower jaw, from the Wind River basin, Lost Cabin beds. The missing teeth are restored in dotted outlines from *D. absarokæ* and *secundus*. Three times natural size.

These three stages afford a clue to the progressive evolution of the *Didelphodus* phylum. The premolars were apparently becoming more complex, the last molar reducing in size. The typical *D. absarokæ* specimens are all from low down in the Gray Bull; *secundus*, from the top of the Gray Bull, probably represents approximately the Lysite stage; while *ventanus* represents the Lost Cabin stage. The New Mexican specimen retains the primitive type of premolar, while its m_3 is reduced. It is probably of somewhat later age than the typical *absarokæ*.

The limited amount and fragmentary character of the material for comparison make it advisable to regard these forms for the present as mutants rather than distinct species.

Pantolestidæ Cope, 1884

Although the teeth are creodont in type, the skull and skeleton of *Pantolestes* described by Matthew in 1909 seem to leave no doubt as to the insectivore affinities of this family. Its Lower Eocene representative, *Palæosinopa*, is nearly allied to *Pantolestes* in dentition, but the upper teeth are more like those of the Leptictidæ (compare especially *Palæictops puercensis* and *Didelphodus absarokæ*) and it retains the paraconid on the lower molars. The characteristic position of the posterior mental foramen beneath m_1 readily distinguishes it from creodonts with similar dentition.

PALÆOSINOPA MATTHEW, 1901

This genus was at first supposed to be a creodont, but the discovery in 1903 of well preserved skeleton material of *Pantolestes* of the Bridger showed that the two genera were nearly related, were widely different from the Creodonta in skull and especially in limbs and feet, and were referable to the Insectivora, although not closely allied to any living families.

More complete material of *Palæosinopa* confirms this arrangement. The limb bones are widely different from those of the Creodonta and agree substantially with those of *Pantolestes*. These distinctions of limb and foot bones, together with the peculiar position of the mental foramen, constitute ordinal distinctions from the Creodonta. In the teeth the resemblance to the Oxyclænidæ, and especially to certain genera of that family, *Oxyclænus*, *Chriacus* and *Deltatherium*, is so close that it is difficult to believe that they can be otherwise than closely allied. But in *Oxyclænus*, *Chriacus*, and *Deltatherium* such parts of the skeleton as are known are of unmistakable creodont type; and, while this may not be accepted by everyone as conclusive against insectivore affinity, it is certainly strong evidence against it, and, in my opinion, decisive. While, therefore, the oxyclænid dentition of *Palæosinopa* and its known insectivore affinity are obviously suggestive of a similar relationship for all the oxyclænid genera, the fact that none of these possesses the peculiarity of a large mental foramen under m_1 and some are certainly creodont-like in limb and foot bones shows that they are not so closely related as the resemblance in teeth would indicate. It does not afford sufficient evidence for removal of any of the Oxyclænidæ to the Insectivora, as suggested by Wortman, although at first thought very suggestive of the change. Nor does it seem to me tenable to place the Pantolestidæ in the same order with the Creodonta.

If the Tupaiidæ and Macroscelididæ (with the Plesiadapidæ, ?Apheliscidæ, etc.) be removed from the Insectivora to a distinct order, Meno-

typhla, as is advocated by some of the highest taxonomic authorities, it would seem necessary also to regard the Pantolestidæ as ordinarily distinct. They might perhaps for convenience be associated with some of the other "Eocene Insectivora" of doubtful position, reviving Cope's name BUNOTHERIA, although not wholly in its original sense. But they do not seem to me to form a natural assemblage.

Three or more species of *Palæosinopa* are represented in the Wasatch collections from the Systemodon zone, chiefly by jaws or parts of jaws, with two very badly preserved and imperfect skulls. A few limb bones are associated with one of the skulls, and a femur with a pair of lower jaws. The femur and tibia agree, so far as preserved, with *Pantolestes*, but the articular ends of both bones are lacking; fragments of the pelvis, axis, lumbar vertebræ, and radius also agree with this genus, but these latter afford no very characteristic distinctions from Creodonta.

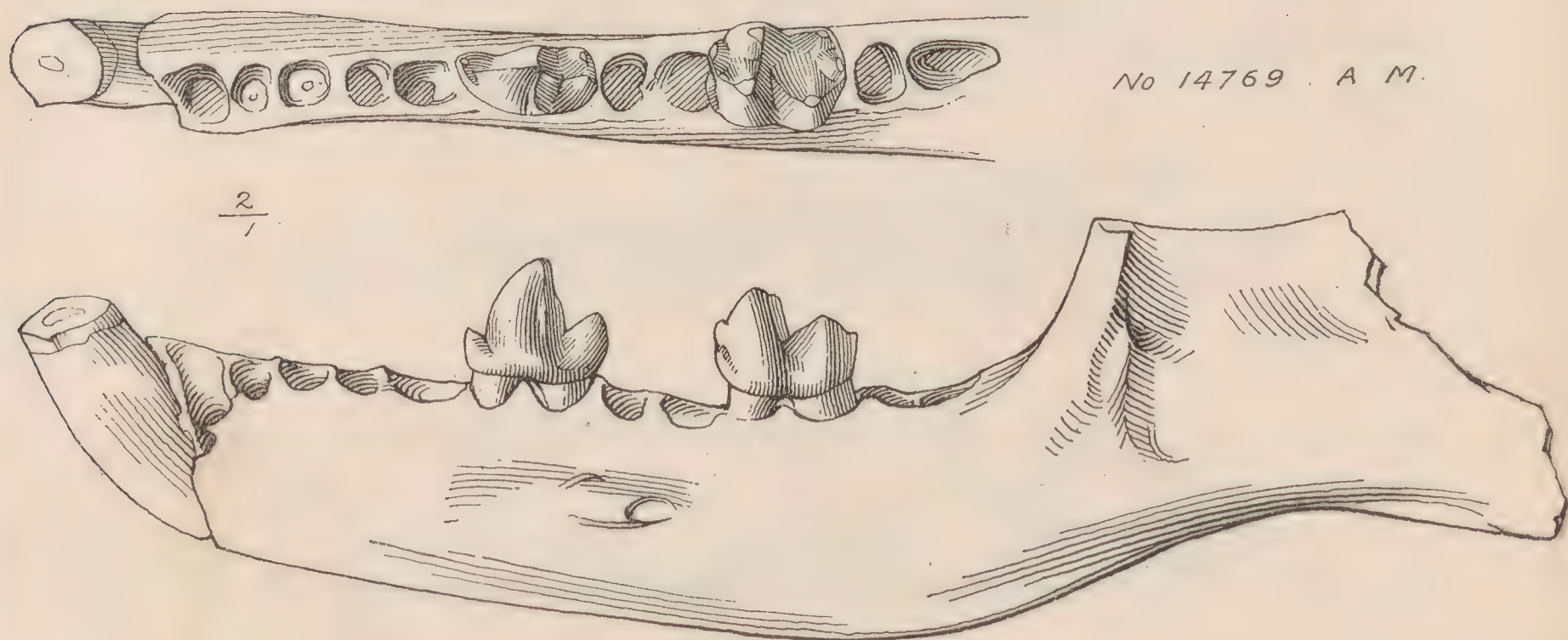


Fig. 16. *Palæosinopa didelphoides*. Lower jaw from the Wind River basin, Lost Cabin horizon; No. 14769. Twice natural size.

The upper dentition has been known hitherto only from the much worn teeth of the type of *P. veterrima*. The unworn teeth are somewhat like those of the Paleocene *Oxyclaenus*. At the same time, the construction of the upper teeth is much more suggestive of leptictid affinities than in the more specialized genus *Pantolestes*. They are tritubercular, with a strong postero-internal cingular ledge; the protocone high and crescentic; paracone and metacone round conic, sharp, somewhat inset from the outer border, with a considerable cingular shelf external to them, and a crest curving forward and outward from paracone apex to postero-external angle. There is a narrow cingulum along the anterior side. The third molar is transverse, the metacone vestigial. The premolars are simple with strong

deuterocone on p^4 and small one on p^3 ; the antero-external and postero-external basal cusps of p^4 are small in one species, vestigial in another.

The species are distinguished as follows:

P. veterrima Matthew. Larger; lower molars more robust; paraconid strong.

P. didelphoides Cope. Lower molars narrower than the preceding; paraconid vestigial.

P. lutreola, new species. Dimensions about two-thirds those of the preceding; posterior mental foramen further back, under posterior end of m_1 .

***Palæosinopa didelphoides* Cope**

Fig. 16

The type is a fragment of the lower jaw from the Wind River (Eotitanops zone). A badly preserved skull, No. 15092, associated with several skeletal fragments from the Bighorn Basin, is referred to this species

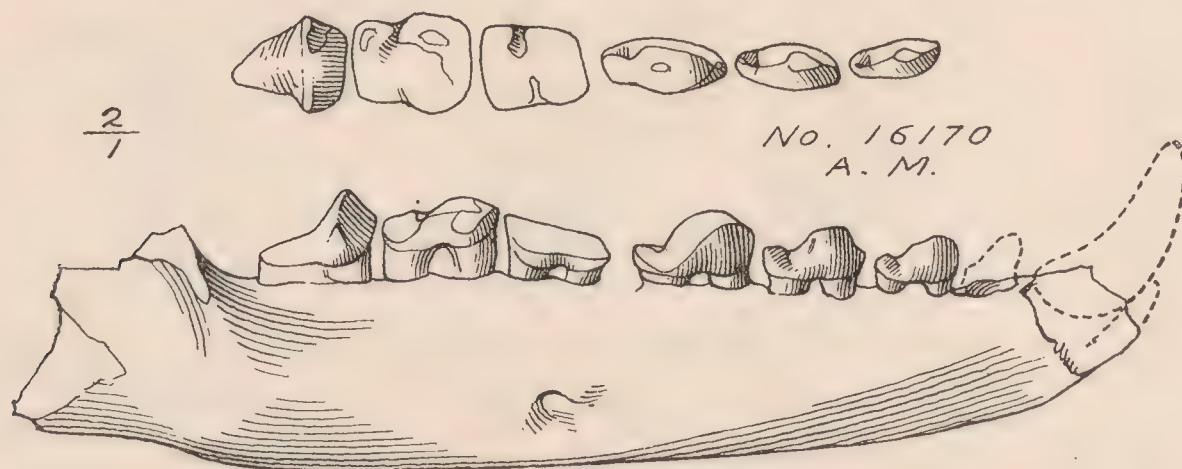


Fig. 17.

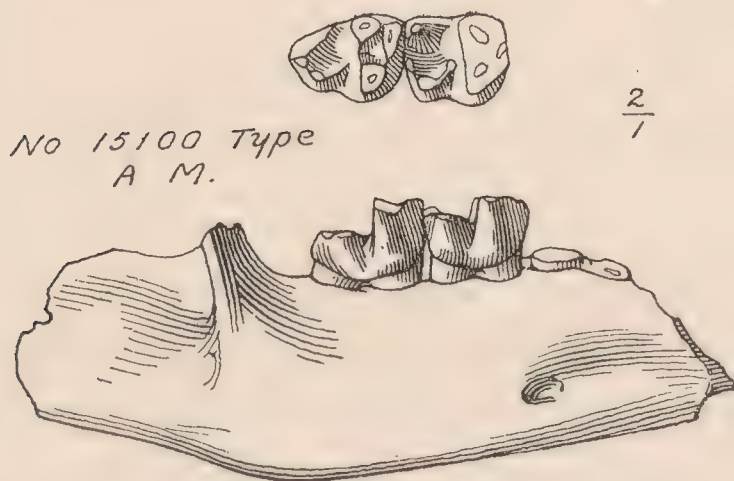


Fig. 18.

Fig. 17. *Palæosinopa lutreola*. Paratype, lower jaw, No. 16170, from the Gray Bull horizon in Clark Fork basin. Twice natural size.

Fig. 18. *Palæosinopa lutreola*. Type specimen, No. 15100. Twice natural size.

provisionally — also No. 15701, lower jaws and femur, No. 15098, part of lower jaw, and other unnumbered jaw fragments all from the *Systemodon* zone. Two other jaws from the Wind River, one of which is here figured, are more certainly referable to *P. didelphoides*.

***Palæosinopa lutreola*, new species**

Figs. 17, 18

Type.— Amer. Mus. No. 15100, part of a lower jaw with m_{2-3} , from Elk Creek in the Bighorn Basin, upper Gray Bull zone of the Wasatch group.

Paratype.— Amer. Mus. No. 16170, lower jaws with teeth much worn, from the lower Gray Bull beds in Clark Fork Basin.

The much smaller size sufficiently distinguishes this species; the posterior position of the mental foramen confirms its generic position. The lower premolar and molar teeth are diminutive copies, both in form and in method of wear, of the larger species.

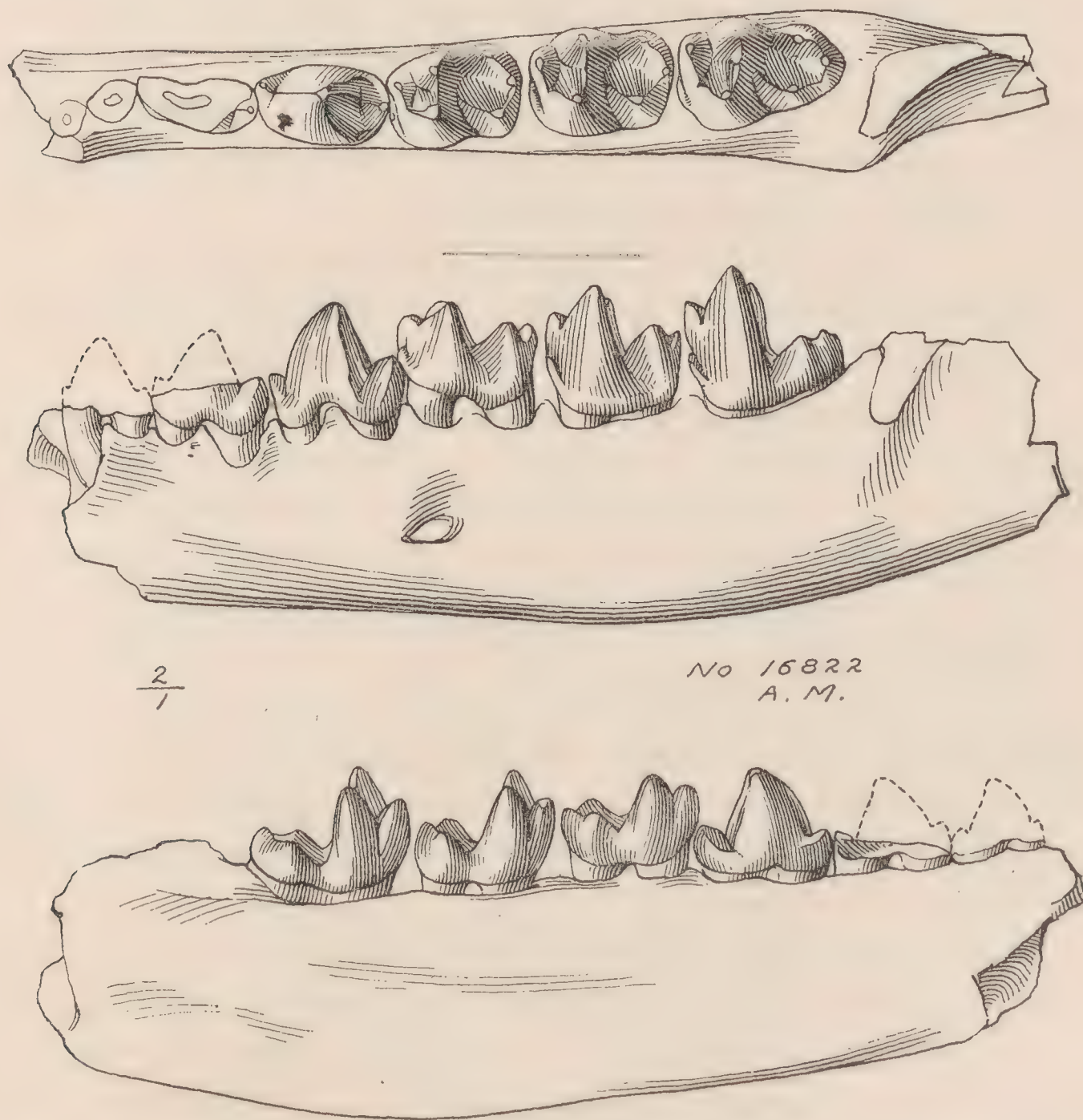


Fig. 19. *Palæosinopa veterrima*. Lower jaw with unworn teeth. Twice natural size.

Measurements

	<i>P. veterrima</i>	<i>P. didelphoides</i>	<i>P. lutreola</i>
Upper teeth, p^3 - m^3 length	23.6	23.6	
Upper molars, m^{1-3} length	13.7	15.0	
M^2 diameters, ant. post. $\times$ trans.	5.0×7.2	5.5×7.8	
M^1 " " "	5.0×7.0	5.0×7.0	
Lower teeth, c - m_3 length		37.4	28.0
Lower molars, m_{1-3}	17.5	15.5	10.4
M_2 diameters, ant. post. $\times$ trans.	5.5×3.8	5.0×3.6	3.0×2.6
Depth of jaw beneath m	10.0	9.5	6.0

Palæosinopa veterrima Matthew

Fig. 19

This appears to be the common species of the genus in the Wasatch, and it is not improbable that the Wasatch specimens above referred to *P. didelphoides* are merely variants of this species. Nos. 15091, 15093-7, 15099, 15733, upper and lower jaws and jaw fragments, agree fairly well with the type, but indicate much individual variability. The greater width of the lower molars, especially m_{1-2} , well developed cusps at the external angles of p^4 , greater transverse width and more triangular form are the distinguishing characters used to separate it.

Dr. Schlosser's opinions in regard to the Pantolestidæ are expressed in the following citation from his memoir upon the Fayûm fauna:

Besides the genus *Sinopa* and its near relative *Cynohyænodon* there might come into consideration as ancestors of *Ptolemaia* also the genus *Palæosinopa* Matthew from the Wasatch beds of Wyoming, which this author now refers to the Pantolestidæ and therewith to the Insectivora. It cannot be denied that it is in fact similar to the genus *Ptolemaia* in the shortness and height of the trigonid and in the size of the talonid of the lower molar, in the triangular form of the upper molar, on which the metastyle appears to be wholly lacking, as well as in the form of the premolars. Matthew is disposed to refer them to the Insectivora, among other reasons, on account of the position of the mental foramen not under the premolars but near to m_1 . So far as this indication is decisive, the lower jaw lying before me can belong to no Insectivore, for the foramen is found here between p_3 and p_4 . On Osborn's original it is not shown.

Reference to the Bridger memoir which Doctor Schlosser cites shows that I devoted several pages to description of the skeleton of *Pantolestes*, and that it was chiefly upon the skeleton characters that the reference of the Pantolestidæ to the Insectivora was based. I pointed out also several Insectivore features in the skull and noted the position of the posterior

mental foramen beneath m_1 (not "near to" it as Schlosser says) as paralleled in many modern Insectivora but not in all: I cited the Insectivores in which it does and those in which it does not occur. At another page of the same memoir I gave a special discussion of the astragalus in various orders of mammals and showed that all Insectivora (including *Pantolestes*) except *Hyopsodus* show certain common fundamental features about the astragalus, all Creodonta and Condylarthra approach another distinct fundamental type, all primates a third, amblypods a fourth, perissodactyls a fifth, artiodactyls a sixth, and so on. I hesitated on this account to accept the reference of *Hyopsodus* to the order by Wortman and Loomis, and have since obtained definite evidence for its removal to the Condylarthra.

My reference of *Palæosinopa* to the Insectivora was not "motiviert" by the position of the mental foramen; in fact, when I first described the genus from the upper and lower jaws I supposed it to be a member of the Hyænodontidæ, where Schlosser is evidently still disposed to refer it. But there can be no question of its near relationship to *Pantolestes*, and the characters of skull and skeleton in that genus absolutely forbid any near relationship to the hyænodonts, particularly to the contemporary primitive hyænodonts of the Wasatch. The teeth of the Pantolestidæ, as I have repeatedly stated, are quite unlike those of any living Insectivora and resemble those of the most primitive creodonts in a very marked degree. But the skull and skeleton are fundamentally unlike the type common to the most primitive members of the creodont-condylarth group, and they do resemble the Leptictidæ and other Insectivora in various criteria which I have cited in the memoir.

A careful study of the dentition in *Palæosinopa* will show that it is not so fundamentally different from *Palæictops* and that the characters of the skull and skeleton in the two conform fairly well.

As for the position of *Ptolemaia*, it seems very probable that the specimen referred to Osborn's genus by Schlosser is an aberrant hyænodont, but after comparing Dr. Schlosser's figures with Osborn's original I cannot believe that they belong to the same or nearly related species. We had of course made careful comparisons of Osborn's type specimen with all the known hyænodonts, and, if it had seemed reasonable to refer it to this family, it would have been so referred. But the molars, although heavily worn, appear to be of a distinct type from any hyænodonts or any other creodont genera; in some degree they suggest Tillodontia, in some degree Pantolestidæ, but not enough to warrant any suggestion of affinities. It seems better to leave it *incertæ sedis*.

Apheliscidæ, new family

Diagnosis.—Jaws slender, lower molars tetracuspid with low trigonid and basin heel, the four cusps submarginal in opposite pairs, equal in height, rounded, m_3 without heel. Premolars simple. Upper molars tritubercular, conules united to wings of protocone, m^3 without metacone. Skull of moderate length, occiput wide, crests low, postorbital process rudimentary, zygomata complete, not heavy. Fore limbs long and slender.

The above cited characters afford a tentative diagnosis. They may not all be of family value; but they will serve to indicate the evidence as to the affinities of this very puzzling animal. It is clearly not closely related to any known genus, living or extinct, and it does not seem practicable to refer it to any known family. Its ordinal relations are very questionable; it is referred to the Insectivora but it may be condylarthran, primate or creodont—in any case a very aberrant type. I hardly think it possible that it could be referred to any other order. There is some suggestion in the teeth of affinity to *Rhynchocyon*, but whether that is wholly due to parallelism or partly conditioned by a somewhat distant relationship is undecided. In any event, the position of the family, if it be insectivore, is more probably among the Menotyphla than any other known groups.

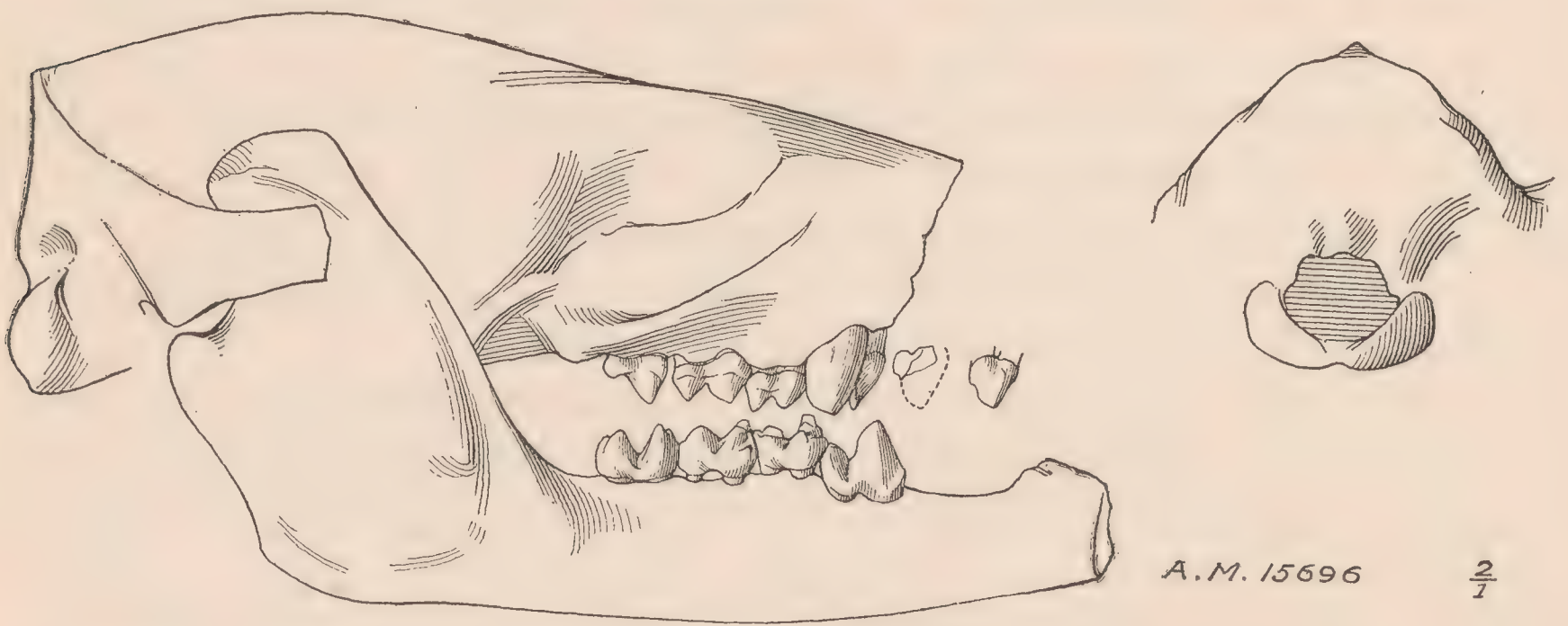


Fig. 20. *Apheliscus insidiosus*. Skull and lower jaw, No. 15696. Right side view, with occipital view of skull, twice natural size.

APHELISCUS COPE, 1875

Type.—*Prototomus insidiosus* Cope, 1874, from Wasatch of New Mexico.

This genus has hitherto been known only from Cope's description and figure of the type specimen, a lower jaw with p_4 – m_3 . The type belongs in

the National Museum collections, but is missing; the figure is very unsatisfactory and the description adds little to it.

A specimen found in the Gray Bull level of the Bighorn Wasatch by the expedition of 1911 agrees with Cope's type, so far as can be judged from the figure and description, and shares with it certain characteristic features that distinguish it from any other Eocene mammal. The trigonid is low, composed of two equal cusps, nearly opposite, rounded, well separated, and barely higher than the heel cusps; the heel basin-shaped, with strong marginal *hy*^d and entoconid, and on *m*₁ and *m*₃ a small hypoconulid; the last molar has no third lobe and the *p*₄ has a large, simple, rather high, somewhat recurved, main cusp and a high heel cusp flattened externally and with a strong transverse ridge from its posteroexternal point, but no basin. These features accord with Cope's figure and description.

The specimen (Figs. 21–24) consists of a crushed skull, lower jaws, and a few bones of the skeleton. It was buried in a hard concretionary mass from which it has been with great difficulty extracted by Mr. Anderson.

The jaw is rather long and slender; the angle of the jaw is not inflected, and appears to be broad and flat. There are four premolars, *p*₃ smaller than *p*₄, *p*₂ much smaller, with rudimentary heel; the front teeth are not very large. In the upper jaw *p*⁴ has two high round-conical cusps, the

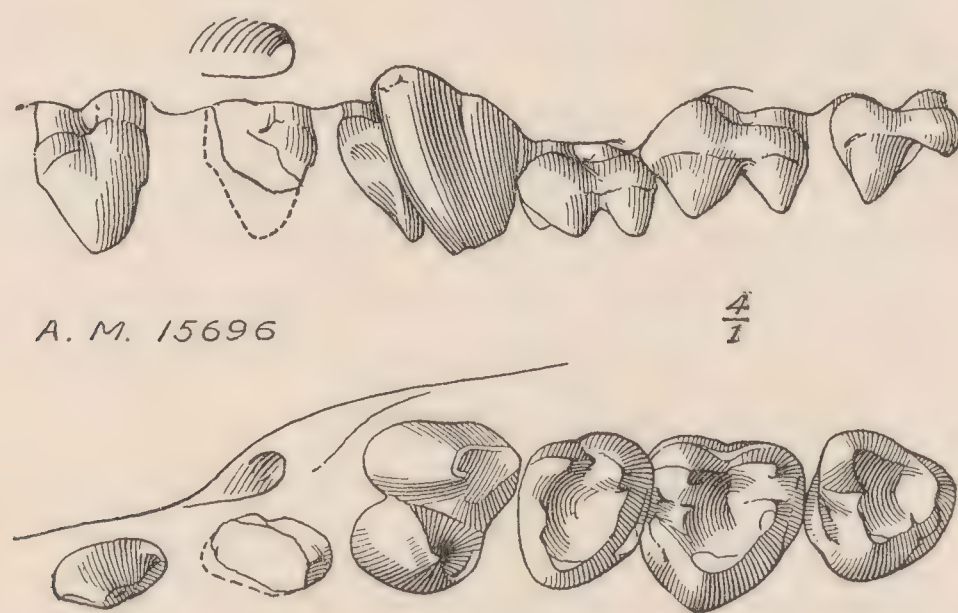


Fig. 21. *Apheliscus insidiosus*. Upper teeth of left side from the skull shown in Fig. 21. External and crown views, four times natural size.

larger external, no heels or basal cingula; *p*²⁻³ are small, simple-crowned with two external roots, the internal cusps and roots absent. The upper molars are of peculiar type. The first two are tritubercular, their transverse width small, conules distinct, protocone large, subcrescentic, the wings of the crescent uniting the conules to the protocone, external cingulum strong, paracone and metacone of equal size, round-conical, wide apart. On the third molar there is no trace of metacone; the paracone and

protocone are high rounded cusps, and behind them is a broad cingular shelf or basin, but no metacone.

There are no indications of marsupial affinities in the above. The genus was referred to the Mesodonta by Cope and where listed is placed under the Notharctidæ (Limnotheriidæ). Its affinities with any genera of known ordinal position are certainly not close, and its characters suggest about equally the tupaoid insectivores, Condylarthra, tritubercular Artiodactyla and several of the Eocene groups of Insectivora.

Description of Skull, Jaws, etc.

Skull.—The front of the skull is broken off obliquely, the fracture passing in front of $p^4 r$ and $p^2 1$. The sutures cannot be certainly distinguished. The orbit is of moderate size, its anterior border above the anterior end of the molar series. The postorbital constriction is wide and short, wholly lacking the narrow elongate proportions characteristic of most typical Insectivora. There is no distinct postorbital process. The postorbital crests are low, obscure, fading out laterally, uniting posteriorly into a narrow, obscure sagittal crest, which becomes distinct but still low and narrow in its posterior third, uniting with the more distinct occipital crest. This crest is not very high and does not overhang the occiput, but extends laterally into the lambdoidal crests, which pass in turn into the upper border of the zygomatic arch. The occiput is broad, flat, not excavated, slopes moderately forward. The basicranial region is so badly preserved that little can be certainly determined; apparently the condyles are rather widely separated, of moderate size and the usual form, the paroccipital process stout and short, the postglenoid process rather weak, the zygomatic arches of moderate depth and not heavy posteriorly.

The *lower jaw* is rather long and shallow; the symphysis is not preserved, so that it must have been wholly in advance of p_2 . The depth of the jaw is greater beneath p_4 than beneath the molars or the anterior premolars. The condyle is low, only a little above the line of the premolar-molar teeth, transversely oval, not wide as in Carnivora and Creodonta; the coronoid process is high, wide, directed more backward than upward, and moderately recurved. The angular process is not well preserved; it is wide, flat and thin, moderately prominent but not extending backward as far as condyle or coronoid, nor downward much beyond the curve of the inferior mandibular border.

Two *cervicals* are preserved, with rather short centra, remarkably small zygapophyses and rather small and weak transverse processes.

The *humerus* is long, slender, the deltoid crest prominent but extending

only a short distance down on the shaft, the distal end wide transversely, with rather large entepicondylar foramen, supinator crest only moderately developed, the distal trochlea rather shallow, the olecranon fossa not deeply excavated.

The *ulna* has a long shaft; the olecranon, although the tip is broken off, was evidently short, weak, and not backwardly directed, the digital fossa is not deep and the radial facet is flat and obscure. The distal epiphysis is gone. It is clear, however, from the proportions that although elongate the ulna was not reduced, the relative proportion to the radius being more as in *Condylarthra* and other primitive types than as in *Creodonta*.

A part of the *ilium* is preserved, but affords few indications of construction other than that the pelvis was elongate, the acetabulum small, weak,

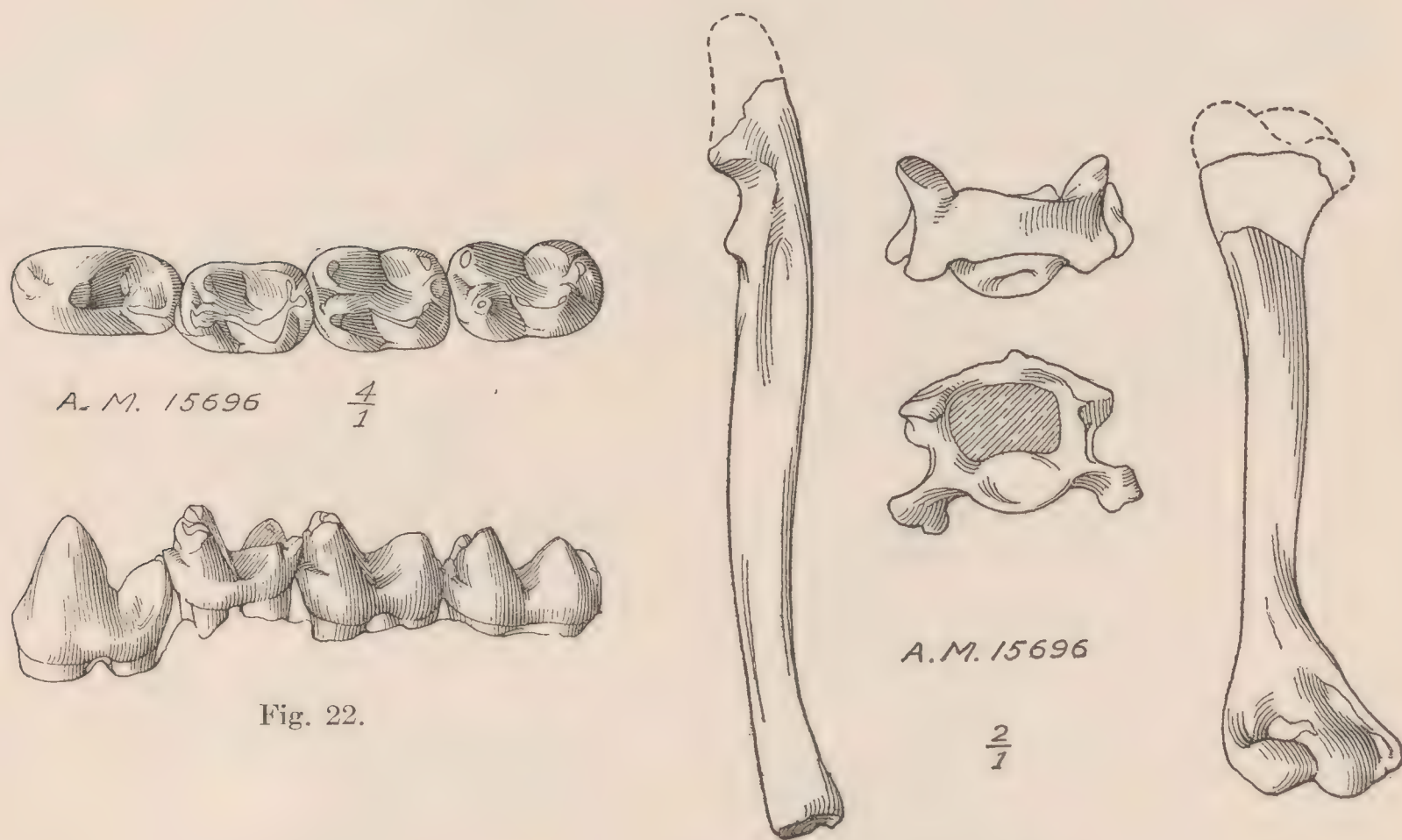


Fig. 22.

Fig. 23.

Fig. 22. *Apheliscus insidiosus*. Lower teeth of left side from the skull shown in Fig. 20. External and crown views, four times natural size.

Fig. 23. *Apheliscus insidiosus*. Bones associated with skull shown in Fig. 20: cervical vertebra, superior and posterior views; right humerus, anterior view; left ulna, anteroexternal view. All twice natural size.

and rather open. There are several other fragments preserved, but so incomplete, broken or distorted by pressure that I cannot obtain from them any data worthy of record.

The above indications point to a long-limbed, weak-jointed skeleton, suggestive rather of lemuroids than of most *Insectivora*, and quite unlike *Creodonta* in its proportions. There is nothing in the skull that points to

the typical Insectivora; the resemblances to that order, such as they are, suggest affinity only to such types as the Tupaiidæ. There is nothing to exclude affinity to the primates, but the long slender jaws, the peculiar type of teeth, the small low brain-case do not favor it. There is nothing except the low-crowned teeth to suggest condylarthran or taligrade affinities, and the construction of these teeth is very remote from any known member of these orders, suggestive rather of the Apatemyidæ in the molars, but in no other particulars.

***Apheliscus insidiosus* (Cope, 1874)**

Figs. 20-24

The skull and jaws, No. 15696, agree in all respects with Cope's type, as far as comparisons are practicable. It thus adds one more to the number of species common to the New Mexican and Wyoming Wasatch. It is from the Upper Gray Bull level. Nos. 34, 44, 4201, lower jaw fragments, are probably from the Gray Bull beds; No. 16925, lower jaw with m_{1-2} from the Sand Coulee beds, and No. 15849, upper jaw fragment with p^4-m^1 from the Clark Fork horizon, are referable to *Apheliscus*. The two latter may represent primitive mutants.

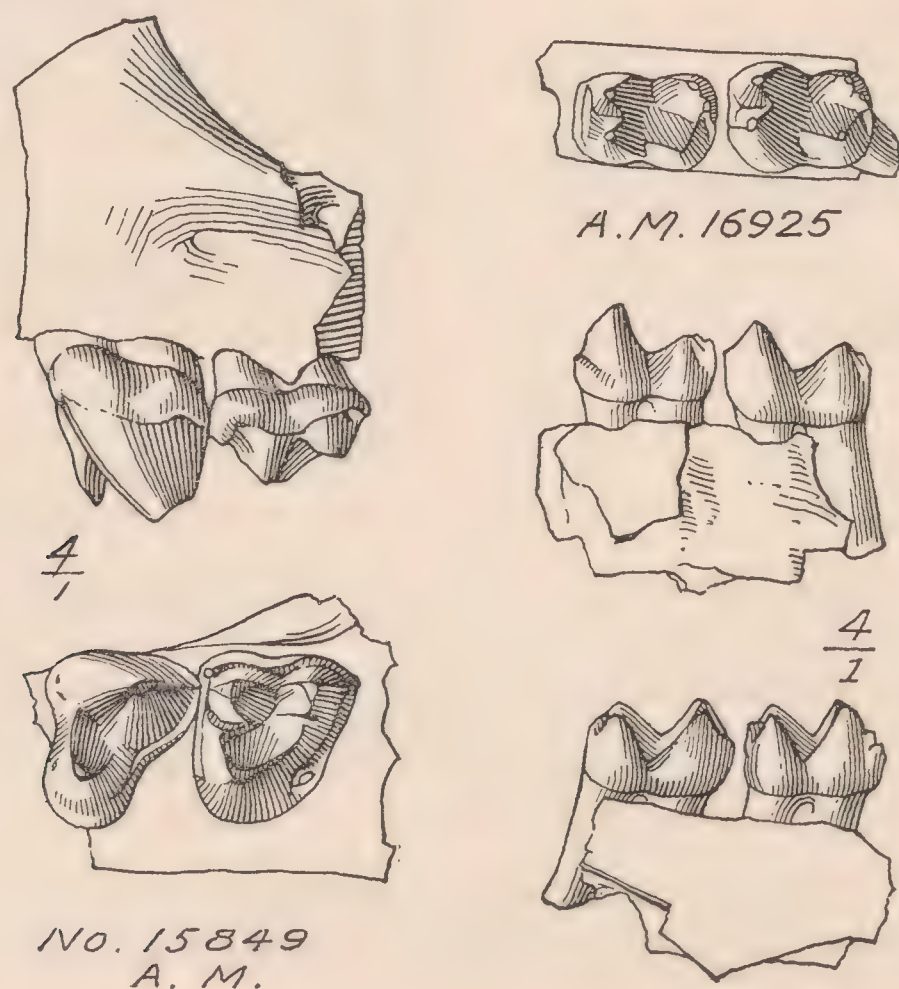


Fig. 24. *Apheliscus insidiosus*?. Upper and lower jaw fragments from Clark Fork and Sand Coulee horizons respectively. These are from a lower geological level than the skull, and may represent primitive mutants. Four times natural size.

? Tupaiidæ

ENTOMOLESTES MATTHEW, 1909

Type.—*E. grangeri* of the Bridger formation, Middle Eocene.

The resemblance to *Tupaia* in the lower jaw and teeth of this genus has been noted by Matthew and Gregory, but until more is known of the animal the reference must remain provisional, as the teeth are of very primitive, unspecialized character, not affording sure grounds of relationship.

Entomolestes nitens, new species

Figs. 25, 26

Type.—Amer. Mus. No. 15697, a jaw fragment with p_4 - m_2 perfectly preserved, from the upper levels of the Gray Bull beds near Fenton in the Bighorn Basin.

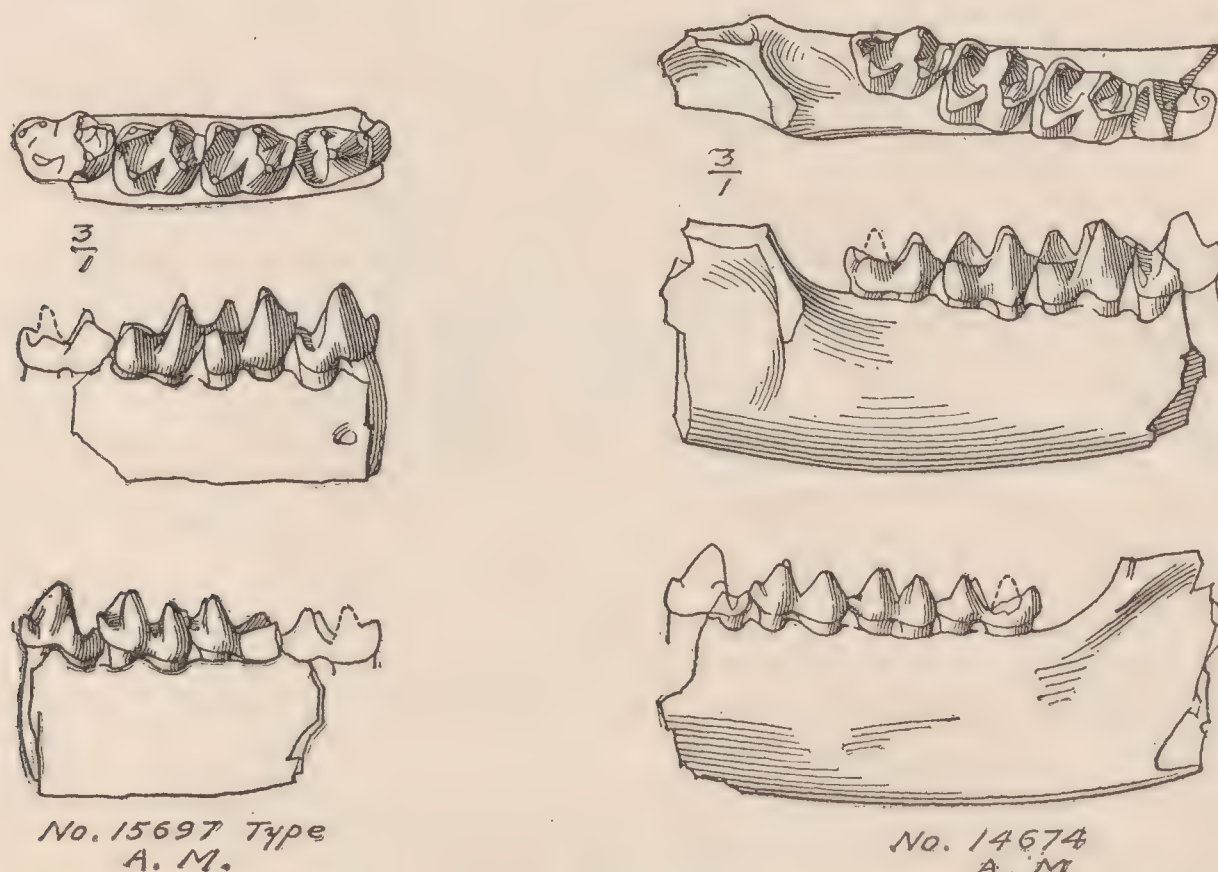


Fig. 25.

Fig. 26.

Fig. 25. *Entomolestes nitens*. Lower jaw fragment, type specimen. Last molar restored in outline from No. 14674. Bighorn basin, upper Gray Bull horizon. Three times natural size.

Fig. 26. *Entomolestes nitens*. Lower jaw from the Wind River basin, Lysite horizon. The fourth premolar is restored in outline from the type. Three times natural size.

Distinctive characters.—One-half larger than *E. grangeri*, p_4 - m_2 = 6 mm.; teeth apparently similar in proportions and construction.

A second specimen, No. 14674, from the Lysite horizon of the Wind River Basin, contains the molar teeth and heel of p_4 . It agrees with the type in all but the larger size of m_2 , which may be of individual or mutative

value. M_{1-3} measures 6.4 mm., the last molar being somewhat reduced. The trigonid is low, with two subequal well separated cusps and a strong paraconid crest; talonid slightly wider than trigonid, with hypoconid and entoconid strong; no hypoconulid except on m_3 , where it is small but distinct. P_4 with small but distinct paraconid and metaconid, and broad, low crested heel.

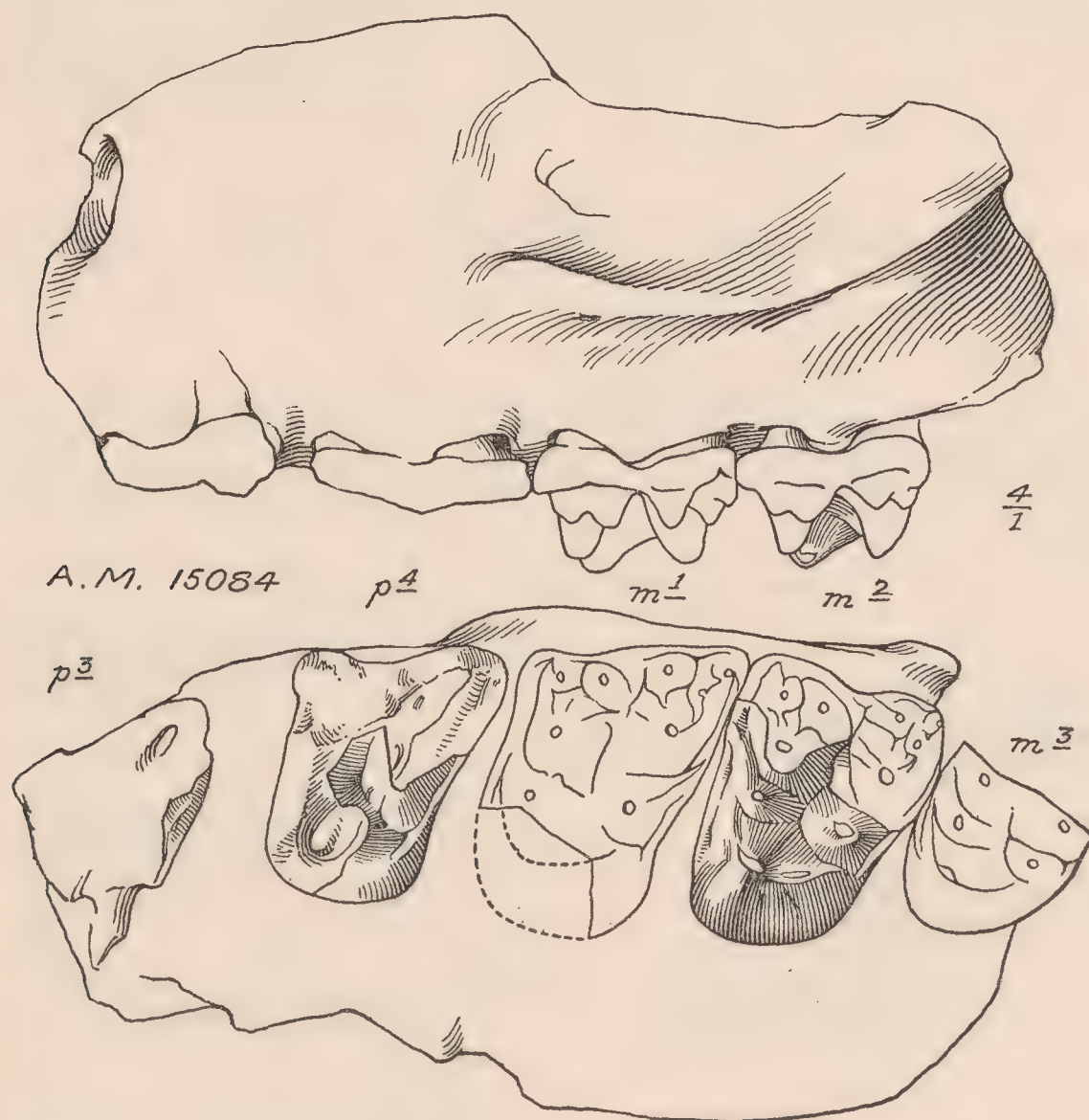


Fig. 27. *Plagiomene multicuspis*. Left maxilla of type specimen, No. 15084, teeth restored in outline from right maxilla and from No. 16166. Gray Bull horizon, Bighorn basin. Four times natural size.

Plagiomenidæ, new family

This family is based upon a genus whose teeth are of very peculiar type, resembling to some extent those of the living genus *Galeopithecus*, inhabiting parts of the East Indies. The new genus is known only from the upper and lower jaws. These show in the molars and posterior premolars certain peculiarities of pattern characteristic of the modern genus. Of the anterior teeth we have only the roots; they are unreduced in number but whether or not they display the peculiar comb-pattern of *Galeopithecus* is unknown.

Some doubt will naturally be felt as to the meaning of this resemblance; the pattern of the cheek teeth is so peculiar and the correspondence so close in the Eocene and the modern genus that I regard it as sufficient evidence

for a provisional phyletic affinity, although not for a positive ordinal reference. Convergence often produces a superficial similarity of form and proportions in the teeth, but I do not know of any instance among mammals where an identical *pattern* in a series of upper and lower teeth of complex construction results from convergence in wholly unrelated types. There is also a certain amount of resemblance in molar pattern to *Myogale*, but it is by no means so close as to *Galeopithecus*.

The anterior teeth, whatever the pattern of the crowns, are entirely primitive in number and proportions, so far as can be judged from the roots and alveoli. These accord in number and proportions with the Eocene Insectivora and related types. There are three small slender incisors, a canine one-rooted and of moderate size, a small one-rooted first premolar, and three succeeding premolars two-rooted, progressively increasing in size, the fourth completely molariform. This is in contrast with the reduced and specialized anterior teeth of *Galeopithecus*. If the modern genus be directly descended, the specialization of the front teeth must have been acquired during the Tertiary, while the peculiarities of the cheek teeth are of more ancient origin. This would be in accord with the relationships

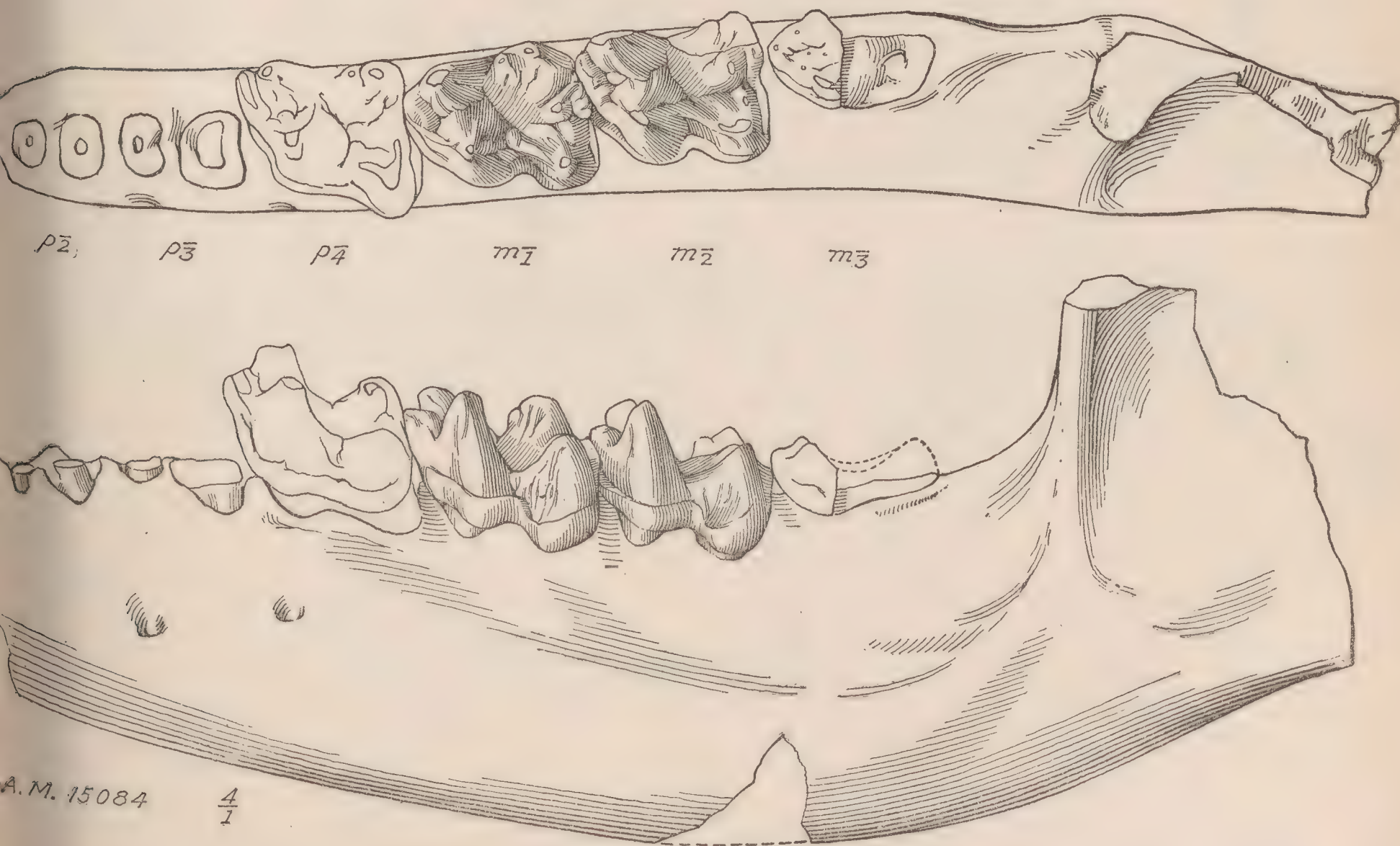


Fig. 28. *Plagiomene multicuspis*. Left lower jaw of type, the fourth premolar restored in outline from No. 15085. Four times natural size.

between Eocene and modern lemuroids. While the pattern of $p_4^4-m_3^3$ is fundamentally the same, it is not identical in detail.

An undescribed genus from the Paskapoo beds of Alberta affords a curious and suggestive resemblance to the new Wasatch genus, and may possibly represent an early stage in the differentiation of its dentition. There is also a certain degree of suggestion, among some of the Lance tribuculate teeth, of affinity to this phylum, but not enough to warrant placing them in it. In the Paleocene no relatives have been recognized.

The more distant resemblance to *Myogale* is perhaps also significant of a real though remote affinity. *Myogale*, while distinctly talpid in its affinities, is considered as in most features a very ancient survival, and *Galeopithecus* is regarded as a peculiar specialization from primitive insectivore stock. This Lower Eocene genus is partly intermediate, helping to bridge the gap.

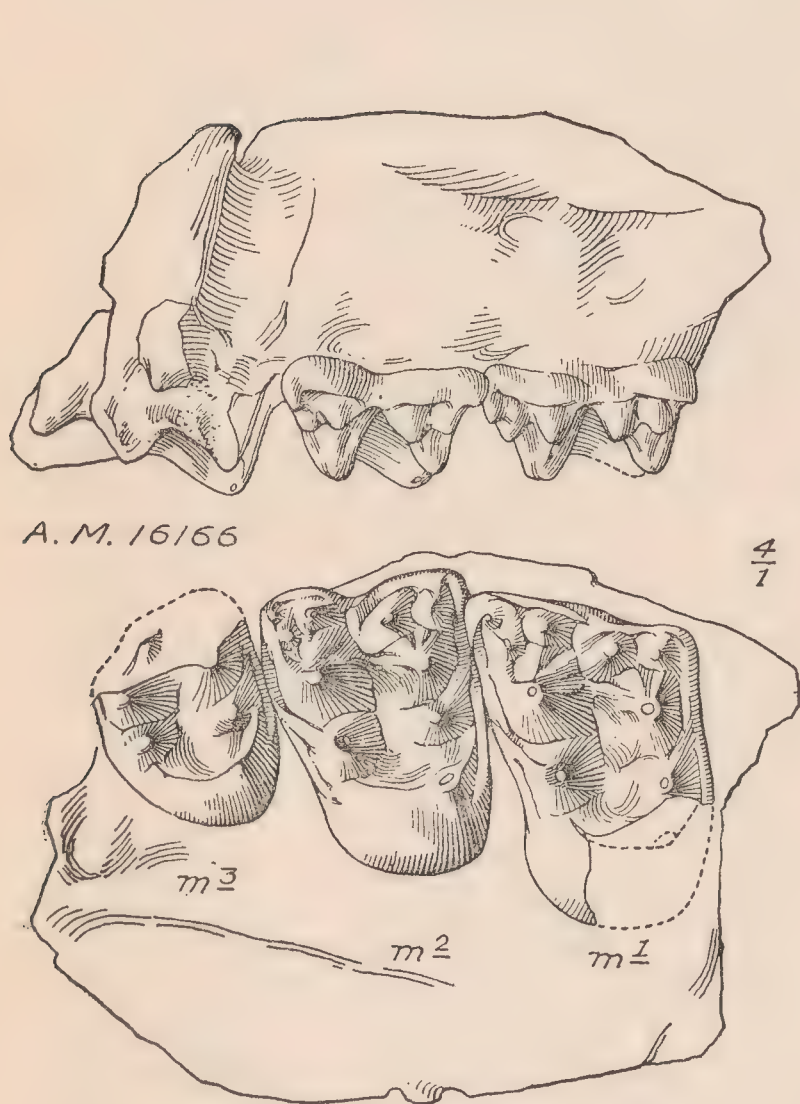


Fig. 29.

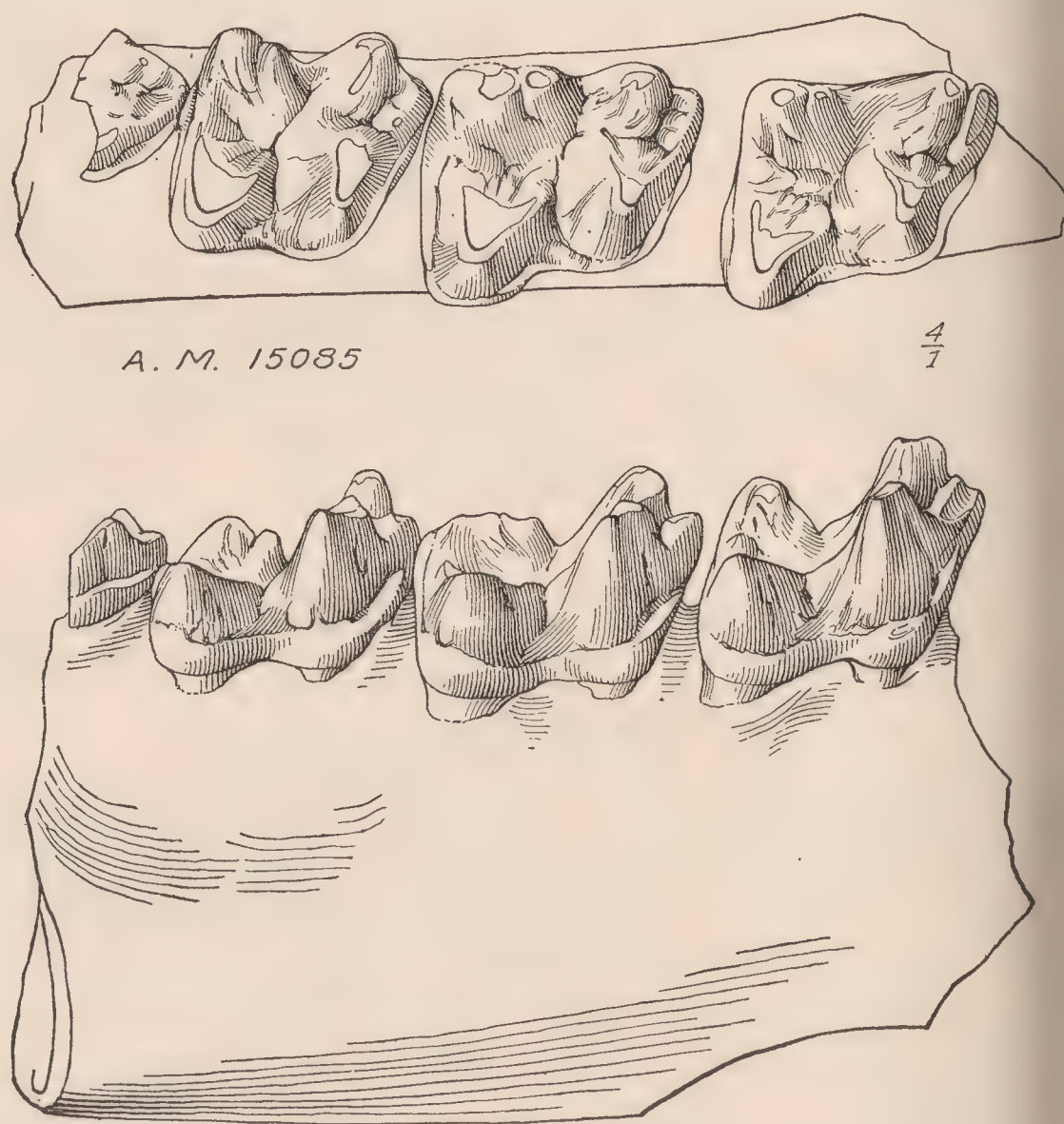


Fig. 30.

Fig. 29. *Plagiomene multicuspis*. Part of right maxilla, No. 16166, with true molars, $m_1^1-m_3^3$. Four times natural size.

Fig. 30. *Plagiomene multicuspis*. Part of right lower jaw with p_4-m_2 and part of m_3 , No. 15085. Four times natural size.

PLAGIOMENE, NEW GENUS

Type.— *P. multicuspis* from the Gray Bull horizon of the Bighorn Basin.

Generic characters.— Dentition $\frac{?.?.?.3}{3.1.4.3}$. Last molar reduced; p_4^4 molariform; lower molars with four principal cusps and a partly connate paraconid, the outer cusps subcrescentic, lower and somewhat posterior to the inner cusps so that the anterior and posterior pair set obliquely and connected by imperfect crests. Upper molars with large crescentic protocone, no hypocone, strong conules, paracone and metacone subcrescentic, a pair of distinct cusps exterior to paracone and a second pair exterior to metacone; a deep valley extending from the outer border of the tooth between the anterior and posterior cusps to the protocone. Three small incisors, canine small, p_3^3 submolariform.

The construction of these teeth is peculiar, unlike any placental molars known to me except those of *Galeopithecus*. The anterior teeth are unreduced and unspecialized so far as the roots indicate.

Plagiomene multicuspis, new species

Figs. 27–32

Type.— Amer. Mus. No. 15084, upper and lower jaws with the teeth mostly broken off.

Paratypes.— No. 16166, upper jaw with m^{1-3} , No. 15085, lower jaw with p_4-m_2 and part of m_3 , No. 15087, lower jaws with p_3-m_3 and roots of front teeth, and part of maxilla with teeth badly preserved. All from the Gray Bull beds of Bighorn Basin.

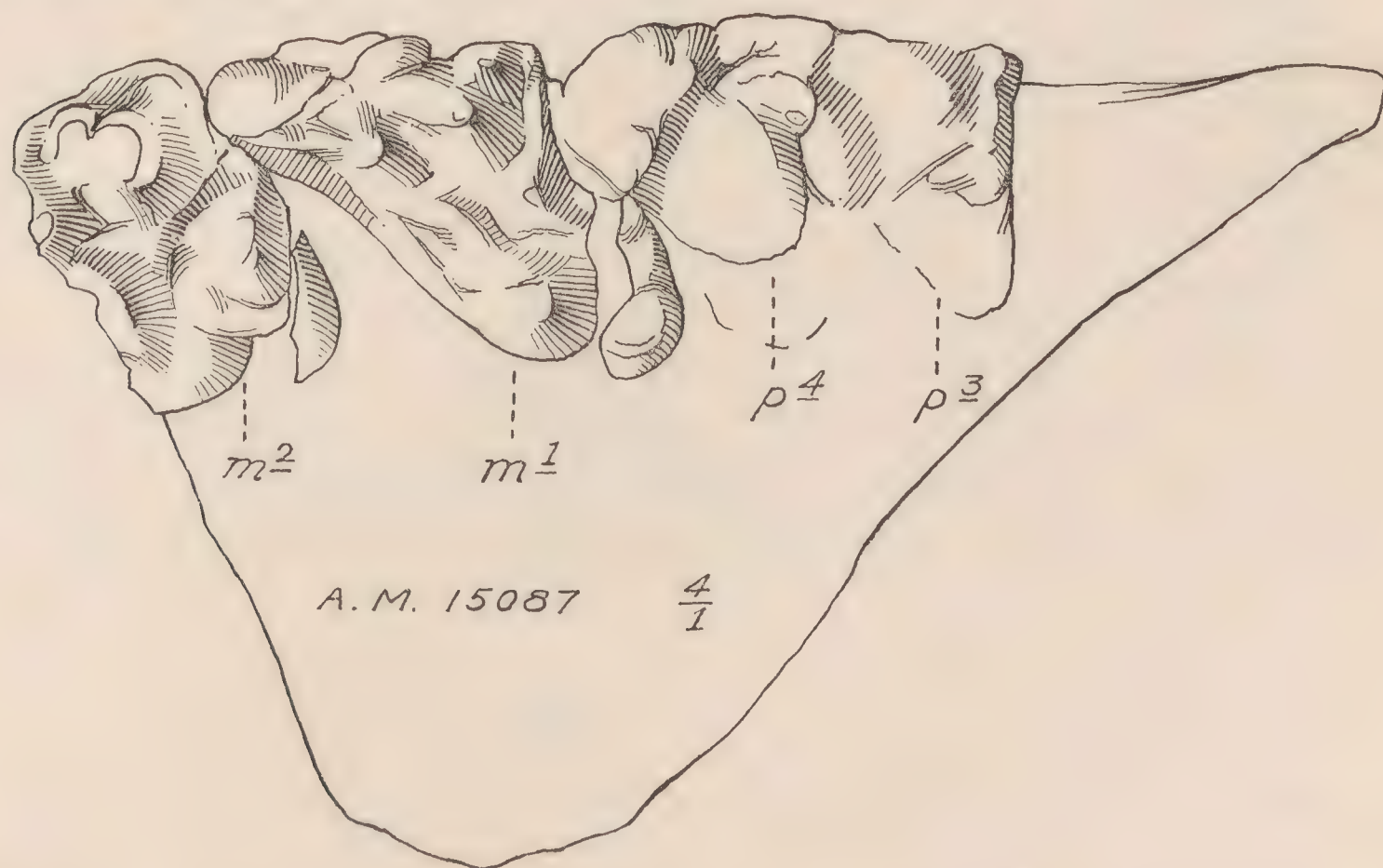


Fig. 31. *Plagiomene multicuspis*. Part of right maxilla with p_3-m_2 badly preserved, No. 15087. Four times natural size.

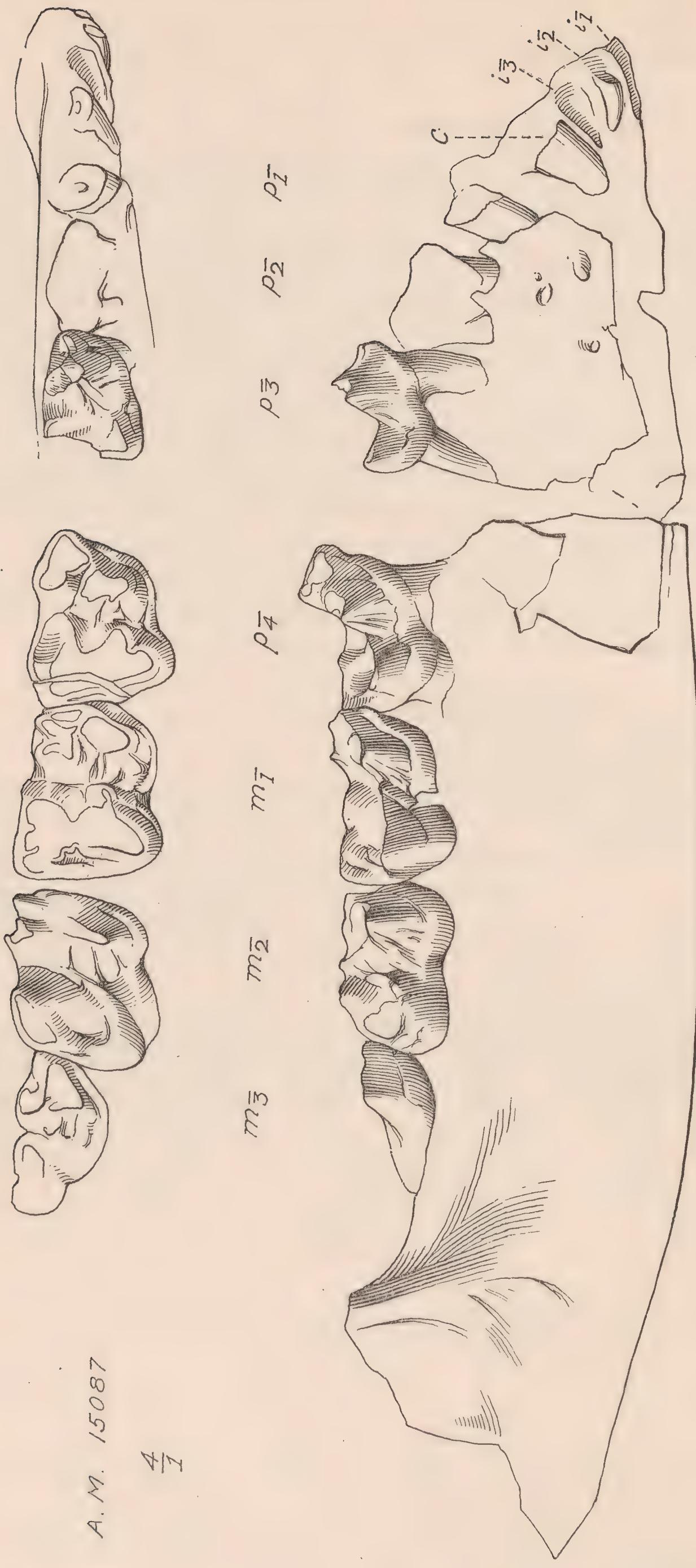


Fig. 32. *Plagiomene multicuspis*. Lower jaw of the same individual as Fig. 32, showing p_3 - m_3 of the right side and roots of the anterior teeth. The characters of the teeth are supplemented from the left ramus mandibuli of the same specimen. Four times natural size.

AFFINITIES DOUBTFUL (?SORICOIDEA OR CHIROPTERA)

NYCTITHERIUM MARSH, 1872

In 1909 I grouped under this genus a number of minute species with molar teeth of the primitive insectivorous pattern common to several groups of insect-eating mammals of diverse affinities. The reasons for referring them provisionally to the Talpidæ were detailed in the memoir on Bridger Insectivora.

A specimen (Figs. 34-35) referred to *Nyctitherium celatum* (*Diacodon celatus* Cope) affords some additional evidence on the affinities of this species. It consists of portions of upper and lower jaws with which are associated three long slender bones, suitable in size and proportions for the shafts of chiropteran fore limb bones, and a few other small fragments not recognizable. Both the jaw parts and associated bones belong to an immature individual, the upper and lower premolars being in a corresponding stage of emergence, and all the remains were found within a few centimetres of each other, in the original matrix. No remains of any other animals were associated with them. The upper and lower jaws almost certainly belong to the same individual. It is highly probable, therefore, that the supposed limb bones likewise pertain to it. Although the supposed limb bones are too incomplete for positive identification, the ends absent or unrecognizable, yet they show clearly an extremely slender, nearly straight shaft, unlike any bone of any terrestrial mammal with which I have compared them. If this identification is correct, as appears reasonably probable, it indicates that this species is a chiropteran; but whether the genus should be referred to that order is still doubtful, in view of the form of the anterior portion of the jaw in some Bridger species (apparently also in this one) the absence of molar cingula, and the conditions of deposition of the Wasatch formation, these conditions making the preservation of an insectivore in its strata far more probable than of a chiropteran. Practically all the positively identified chiropteran fossils have come from cave or fissure formations; the Wasatch is a river-valley formation. For these reasons I have preferred not to transfer *Nyctitherium* to the Chiroptera, although its known remains are very suggestive of affinity to the bats.

Nyctitherium celatum (Cope, 1875)

Figs. 33-34

Diacodon celatus, COPE, 1875, Syst. Cat. Eoc. Vert. New Mex., p. 12; 1877, Ext. Vert. New Mex., p. 133, Pl. XLV, fig. 20.

?*Synonym*.—*Anaptomorphus minimus* LOOMIS, 1906.

Type.—U. S. Nat. Mus. No. 1126, lower jaw with m_{1-3} , from the Wasatch of New Mexico.

Although referred by Cope to *Diacodon*, this species apparently does not belong in the Leptictidæ but to the group of minute species which I have assembled under *Nyctitherium*.

No. 15103, lower jaws and upper molars associated with parts of limb bones, is referable to Cope's species. It is from the middle Gray Bull beds

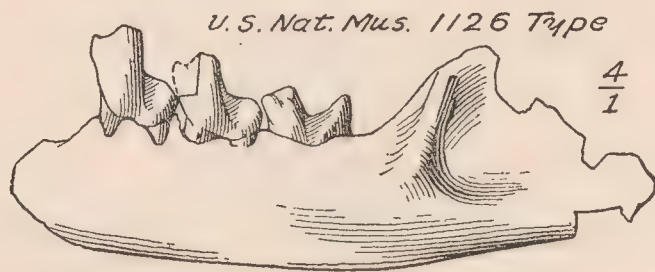


Fig. 33. *Nyctitherium celatum*. Lower jaw, type specimen, U. S. National Museum, No. 1126. Wasatch of New Mexico. Four times natural size.

of the Bighorn Basin and shows the last milk molar and first two true molars of upper and lower dentition.

The molar teeth are much like those of *Vespertilio* in proportions and construction, but have no external cingula. Trigonid wide and short, protoconid and metaconid subequal, opposite, paraconid small, low-set, not projecting far forward; heel as wide as trigonid, short, hypoconid and entoconid wide apart, equal in height, their points at about the same level as paraconid; no hypoconulid; cusps sharp, angulate, basins deep.

The milk molar is a smaller, narrower tooth than m_1 , similar in construction.

The upper molars are sharp-cusped, triangular in form, with subequal paracone, metacone, and protocone, external angles extended into sharp styler cusps, and a well-developed hypocone at a lower level. The paraconule and metaconule are sharp, although low-set, the mesostyle distinct but small. The three principal cusps with the parastyle and metastyle outline a sharp oblique triangle.

The anterior portion of the lower jaw is broken off in front of dp_2 . A part of this tooth is preserved and apparently projected strongly forward.

The posterior end of the symphysis is more doubtfully indicated; it appears to be of the long loose type characteristic of many Insectivora, quite unlike anything in the Chiroptera.

If this species be really chiropteran it had the long slender symphysis which Schlosser ascribed to *Vespertiliavus*.

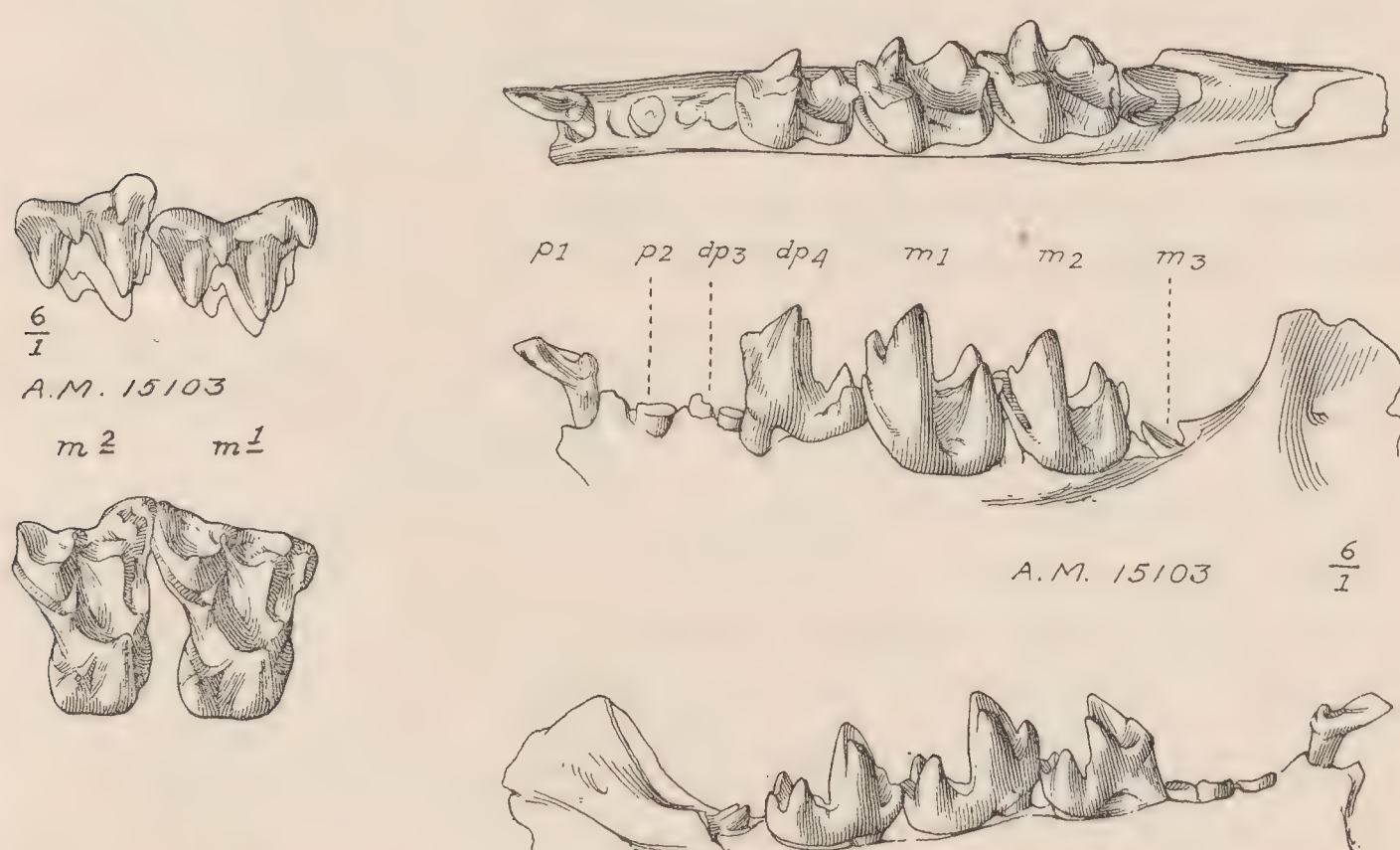


Fig. 34. *Nyctitherium celatum*. Upper teeth, m^{1-2} of the right side, external and crown views, and lower jaw of the same individual crown, external, and internal views of the left ramus, six times natural size. No. 15103, from the Bighorn basin, Wyoming. With this are associated certain supposed chiropteran limb bones.

WINGE ON AMERICAN EOCENE INSECTIVORA

Winge has recently published a review of the mutual affinities of the Insectivora¹ in which he discusses the position of various American Tertiary genera. His conclusions differ — in some cases differ widely — from those of most palæontologists and, although very positively expressed, are in some instances quite untenable.

The following translation expresses his views:

Near to the Galeopithecidae, originating from a family of very primitive forms, stands a little group of mutually near-standing North American families, all extinct in the Tertiary period: Leptictidae, Tillotheriidae, Periptychidae and Stylinodontidae.

¹Winge, 1917. Udsigt over Insektædernes indbyrdes Slægtskab. Vidensk., Medd. fra Dansk naturh. Foren., LXVIII, pp. 83-203.

The peculiarity that unites these American families with the Galeopithecidae and places them at a lower stage in specialization than all other members of the Insectivore order, is that they have normally proportioned nasal cartilages; the nasals were not or scarcely at all tubular, to judge from the form of the facial bones, and the nasal muscles have not impressed their attachments upon the cheek arches or in other ways moulded their environment. A peculiarity that is common to the named American families and sets them upon a higher stage [of development] than the Galeopithecidae, is that the intermediate, second, of the three outermost cusps [i. e. mesostyle] upon the upper molariform teeth has disappeared, and that the 4th and 5th cusps [parastyle and metastyle] have lost more or less of the V-shape and become conical.

Lowest among the named American families stands the Leptictididae [Leptictidae] with the genera *Ictidops* [*Ictops*] and *Leptictis*, both genera with assuredly mouse-like body form.

Ictidops [*Ictops*] with *Palæictidops* [*Palæictops*] ¹, which is known from the anterior part of the skull, with lower jaws, is in some respects the most primitive of the genera: all three upper incisors are present; upper P³ has intermediate form with inner heel; the temporal crests unite in a sagittal crest. It appears otherwise to be very close to the better known *Leptictis*. Upon the upper molariform teeth the 7th cusp [hypocone] may be proportionately of considerable size and the intermediate cusps [conules] can be found upon the anterior and posterior borders [wings] of the 6th cusp [protocone]. In the lower jaw, p₄ is molariform, with the primitive five cusps; upon the remaining molariform teeth, the 1st cusp [paraconid] appears to be much reduced or wanting. The lower jaw has a rather primitive form, elongate and slender with strong coronoid process and quite small angular process; its condyle lies at a level scarcely higher than the cheek teeth.

The following comments may be made upon the above. *Ictops* is an Oligocene genus, *Palæictops* a Lower Eocene and Paleocene genus. *Ictops* is known from many complete skulls and most of the skeleton; the skull of *Palæictops* (*Diacodon*) is figured in this article. *Ictops* has, like *Leptictis*, two upper incisors and separate temporal crests; *Palæictops* (= *Diacodon*) has three upper incisors and a single sagittal crest. The cheek teeth in the two genera are practically identical. (All these data are to be found in previously published articles by Cope, Leidy, Scott, Douglass and myself.) Whether the construction of the molars is a derivative of that of *Galeopithecus* or vice versa appears to the present writer to be purely speculative. Both types are present in the Lower Eocene (*Diacodon*, *Plagiomene*), and if the leptictid type is recorded from the Paleocene while the other is not,

¹ Dr. Winge appears to be somewhat hypercritical in these emendations. He has himself proposed the name Amphictidae and finds no difficulty in accepting *Icticyon*, *Ictitherium*, etc. His emendation of Leptictidae is technically correct; the emendations of *Ictops* and *Palæictops* are not warranted, since in these instances the names are compounds presumably with the first syllable of *Ictis*, not with the whole word. *Ictidops* was proposed by Broom for a genus of Permian reptiles, but on this understanding is not preoccupied by *Ictops*.

it is probably a mere matter of accident, for a type of dentition which approaches the galeopithecoid is found in the still older Lance. The zalambdodont and soricoid types of teeth appear to be equally ancient, and we know too little about the Mesozoic mammals for their phyletic relations to the early Tertiary types to be any better than conjectural.

Winge's arrangement of the Insectivora appears to be solely upon the basis of his theories of cusp evolution, and it is for this reason alone, as far as one can judge, that he places the highly specialized and peculiar *Galeopithecus* at the base of his phyletic tree. Undoubtedly there is a great deal of truth in Winge's insistence upon the antiquity of the outer cusps or styles in some at least of the mammalian races. But I have never believed that any one order of cusp evolution applies to all mammalian phyla, and the absurd results to which an uncritical dependence upon any theory of this kind will lead, are very well illustrated in the paper cited.

So far as the Leptictidæ are concerned, they are undoubtedly related in the structures of skull, teeth, and skeleton to the Erinaceidæ, share some of the specialized characters diagnostic of that family, and are not remote in dentition from such primitive genera as *Proterix*, *Gymnura* and *Hylomys*. *Ictops*, however, at least, has a true ossified tympanic bulla, delicate and loosely united to the skull so that it is only occasionally preserved; none of the genera have any false (alisphenoid) bulla.

Much may be said likewise in favor of including the Tillodontia among the Insectivora, so long as one considers only the teeth. The skulls and skeletons of *Esthonyx* and *Tillotherium*, so far as I have examined them, afford no diagnostic insectivore characters. They share indeed a great many primitive characters with some or all of the Insectivora. But the same may be said of all Paleocene and most Lower Eocene mammals. If they are not allowed a separate order, their most convenient place is doubtless with the Insectivora.

The inclusion of the Periptychidæ (including the Mioclænidæ but exclusive of *Ectoconus* which Winge refers to the Condylarthra) and of the Tæniodonta in the Insectivora, and the characterization of them as forming with the leptictids and tillodonts "a little group of closely related families," are, however, quite impossible, and deserve almost to be ranked with the taxonomic eccentricities of Steinmann and Jaekel. It is difficult to find in Winge's discussion of them any real reasons for associating any of these families with the Insectivora, except a recognition that the teeth are all more or less of the "tritubercular" type or clearly derivatives from it. But this is true of all early Tertiary mammals, a fact upon which American palæontologists have been insisting for many years. The earliest creodonts, condylarths, perissodactyls, artiodactyls, primates, amblypods, etc. show

this derivation quite as clearly. On the other hand, there are marked differences in skull and skeleton structure, especially in the characteristic construction of manus and pes, among types which are often difficult to distinguish by their cheek teeth; and, for this reason, the teeth alone are not a safe guide to affinities. Winge apparently attaches little weight to these features; and he wholly ignores another important part of the evidence, the relative geological age of the various genera. All of them in his view are from the "American Tertiary." In other words, his derivations are purely structural, not genetic, and he makes no use at all of the direct or approximate genetic phyla which have been studied so extensively in this country and elsewhere, and which should serve to test and check his theories of structural derivation.

The results of such checking of theories by facts would be somewhat unfortunate for certain of his views upheld in this paper and elsewhere. He regards the outer styles of the upper molars as original elements, and ranks those genera which have them strongly developed as more primitive than those in which they are weak or absent. Now many instances can be cited among phyletic series which are *known* to be true series by the succession in time and gradual modification in *all parts of teeth, skull and skeleton* from the first to the last member, in which the styles are progressively developed — none in which they progressively disappear. He regards the molariform fourth premolar as primitive and the simple fourth premolar as a derivative of it. Many true genetic series can be cited which show the fourth premolar becoming progressively molariform — none in which it is at first molariform and becomes progressively simple.¹

With regard to the Periptychidæ and Mioclænidæ, the facts are as follows: *Ectoconus*, which Winge says is known only from parts of the jaws, is in fact known from a complete skeleton not yet described, but some characteristic bones of the skeleton were described many years ago. *Periptychus*, which he says is known only from pieces of upper and lower jaws and a few isolated parts of the skeleton, is, in fact, known from the greater part of

¹ It might be objected indeed that the succession of genera forming these phyla were arranged in it upon the theory that the fourth premolar, at first simple, has become molariform; that if arranged upon the opposite theory, an entirely different collation of genera would result; that the validity of the phyla depends therefore upon the validity of the theory of cusp sequence. But in every instance where the skulls and skeletons are completely known, the validity of the accepted arrangement is confirmed by the coordinate gradual modification of all other parts of skull, vertebræ, limbs and feet, so that it is amply proven to be correct.

Winge's theories have their place among other speculative hypotheses as to the origin of the several types of dentition that we find at the beginning of the Tertiary. But as a guide to the affinities of Tertiary and modern orders they are wholly misleading. It is noteworthy that Winge, Ameghino, and other authorities who have maintained various peculiar views as to the evolution of the mammalian molars, have either disregarded the evidence of the geologic succession or have been compelled to distort it in order to maintain their theories.

the skull, complete lower jaws, and the hind limb and foot and other parts *associated*¹ in every instance with the characteristic jaws and teeth. Both genera show throughout the skull and skeleton, and especially in the very characteristic construction of tarsus and phalanges, an unmistakable affinity to *Pantolambda*, also known from the complete skeleton, and through *Pantolambda*, are connected with the Amblypoda. The specific points of resemblance were stated by Osborn in 1898; much confirmatory evidence is afforded by the more complete specimens obtained in the last few years. They are not unguiculates but ungulates; the construction of the tarsus, while much less specialized than in *Coryphodon*, is very clearly advanced in that direction as compared with any generalized forms ancient or modern.

As to the smaller Periptychidæ, they are known chiefly from the jaws and poorly preserved skulls. The few diagnostic fragments of the skeleton show that they differed considerably from *Periptychus* in spite of the resemblance in teeth, but there is no evidence sufficient to disprove their reference to the same family.

Mioclænus and its relatives are also known chiefly from the jaws and poorly preserved skulls; a few characteristic fragments of the skeleton show that the tarsus was more like that of the condylarths and early creodonts than that of Periptychidæ. The teeth do not resemble the Periptychidæ in any of the features of construction special to that group. Herein they differ from the smaller periptychid genera. The premolars indeed are more or less enlarged and inflated, and it appears to be upon this single feature, not peculiar to the Periptychidæ, that Winge bases his union of the Mioclænidæ with that family. But in details of molar and premolar construction the Mioclænidæ are much closer to the earliest phenacodonts, the hyopsodonts and the creodont oxyclænids.

All of these Paleocene groups differ widely in skull and skeleton structure as well as in teeth from the contemporary Leptictidæ, also known from the complete skeleton, in which tibia and fibula are coössified distally, the astragalus of the characteristic insectivore type with broad shallow short trochlea defined internally by a sharp crest, no astragalar foramen, etc.

The position of the Tæniodonta is not so clear. Dr. Winge regards them as all representing one phylum and does not hesitate to derive the Puerco "*Hemiganus*" (= *Wortmania*) from the Torrejon *Conoryctes*. In fact they represent two distinct phyla diversely specializing; *Conoryctes* is decidedly more specialized in most characters than the older *Hemiganus*, but in a

¹ I. e., positively known to belong to the same individual.

different direction. The oldest stages of each phylum, *Onychodectes* and *Wortmania*, both have very primitive teeth, but little different from the Creodonts; but the astragalus of *Onychodectes* and the metapodials of *Wortmania* differ much more from the creodont type and approach the primitive edentate type as exemplified in the armadillos. This may, however, be a matter of parallelism; the evidence is not sufficient to decide. The further specialization of the stylinodont phylum, superficially resembling the ground-sloths, is unquestionably a matter of parallelism. It is unfortunate that all the arguments presented by Scott, Winge and Ameghino against the edentate affinities of the Tæniodonta have been directed against the quite untenable position that the stylinodonts were the direct ancestors of the ground-sloths. It is a simple matter to show that this could not have been the case; no palæontologist save Wortman has maintained that they were so. But this does not at all disprove the view that they were a side branch from primitive armadilloid edentates, from near the base of the ordinal phylum, the stylinodonts paralleling the ground-sloths, the conoryctids paralleling the armadillos. This is the view tentatively held by Dr. Wortman's colleagues, whom Winge cites as accepting Wortman's own conclusions. The arguments pro and con will be presented in describing the more complete tæniodont material recently secured by the American Museum expeditions. It is sufficient for the present to observe that none of the arguments presented by the three writers above mentioned are in any degree valid against it. It might seem that Winge, who admits *Manis* and even *Orycteropus* to the Edentata, is quite unduly critical in excluding the tæniodonts and even Metacheiromyidæ from the order; but an examination of his argument shows that his acquaintance with them is rather slight and not altogether accurate.

It must be observed, however, that the reference of the Metacheiromyidæ and tæniodonts to the Edentata, *sensu lato*, which I have advocated, does not exclude affinity to the Insectivora. I regard the two orders as derived from a common Cretaceous ancestry and their representatives in the Paleocene as rather nearly related — more nearly, perhaps, than to the condylarth-creodont group or the taligrade-amblypod group or the primate group. Dr. Winge is by no means so far wrong in referring the tæniodonts to the Insectivora as he is in referring the peripitychids to this order.

ORDER AND AFFINITIES UNCERTAIN

CREOTARSUS,¹ NEW GENUS

Type.—*C. lepidus*, *infra*.

Generic characters.—Dentition $\overline{??.4.3}$. P_1 one-rooted; p_{2-4} two-rooted, subequal, spaced, p_4 with strong well separated metaconid (deuteroconid), small paraconid and broad short heel. Molars with protoconid and metaconid of equal height, widely separate, paraconid small, low, internal in position on m_1 , doubtfully present on m_{2-3} . The trigonid is rather high and wide; talonid basined, equal in width to trigonid; hypoconid strong, set well out; entoconid marginal, small; hypoconulid rudimentary. M_1 and m_2 similar in size and construction; m_3 longer, with (?narrow) heel. Canine probably small; incisors unknown. Jaw slender, elongate, with broad angle not incurved. Posterior mental foramen beneath anterior part of p_3 . Tarsus of creodont type in some particulars; the astragalus with oblique, moderately grooved trochlea, distinct astragalar foramen, calcaneum with well-marked fibular facet, cuboid with astragalar facet of moderate width, shaped as in Artiodactyla. Metatarsal IV of moderate length, its facets and those of the cuboid indicating a well developed (unreduced) Mt. V.

The ordinal position of this genus is very doubtful. The peculiar astragalo-cuboid articulation approximates the characteristic type of the Artiodactyla; but the astragalus exhibits very slight approach, if any, to the artiodactyl form. The calcaneo-fibular facet has not the peculiar form and relations seen in that order; it is much more like the corresponding facet in *Limnocyon* and other creodonts. The long slender jaw, spaced and rather long premolars, and the construction and proportions of the molars are suggestive of *Diacodexis*; but the peculiar double-cusped p_4 is quite unlike any of the genera positively known to be dichobunids,² while suggesting Insectivora or Condylarthra. While it is not impossible that it has some affinities to the Artiodactyla, this appears unlikely.

Comparison with the Condylarthra is equally unsatisfactory. There are no very decisive characters in the teeth and jaw to exclude it from this order, but there is certainly nothing characteristically condylarth about them; in the tarsus, the astragalus agrees fairly well, but the peculiar cuboid and the broad fibular articulation are unlike the known groups of this order.

¹ Creodonta, *ταρσους*, foot, in reference to the creodont type of tarsal bones.

² But compare *Sarcolemur*.

From the Creodonta the genus is distinguished by the general type of molars and p_4 , and the small canine (inferred from the slenderness of the jaw under p_1); the tarsus is of creodont type; the peculiar naviculo-cuboid facet is of somewhat the same type as in the Mesonychidæ; but there is no near approach to any one of the creodont families in the tarsal construction.

Primate affinities are excluded by the long slender jaw, and the radically different type of tarsus.

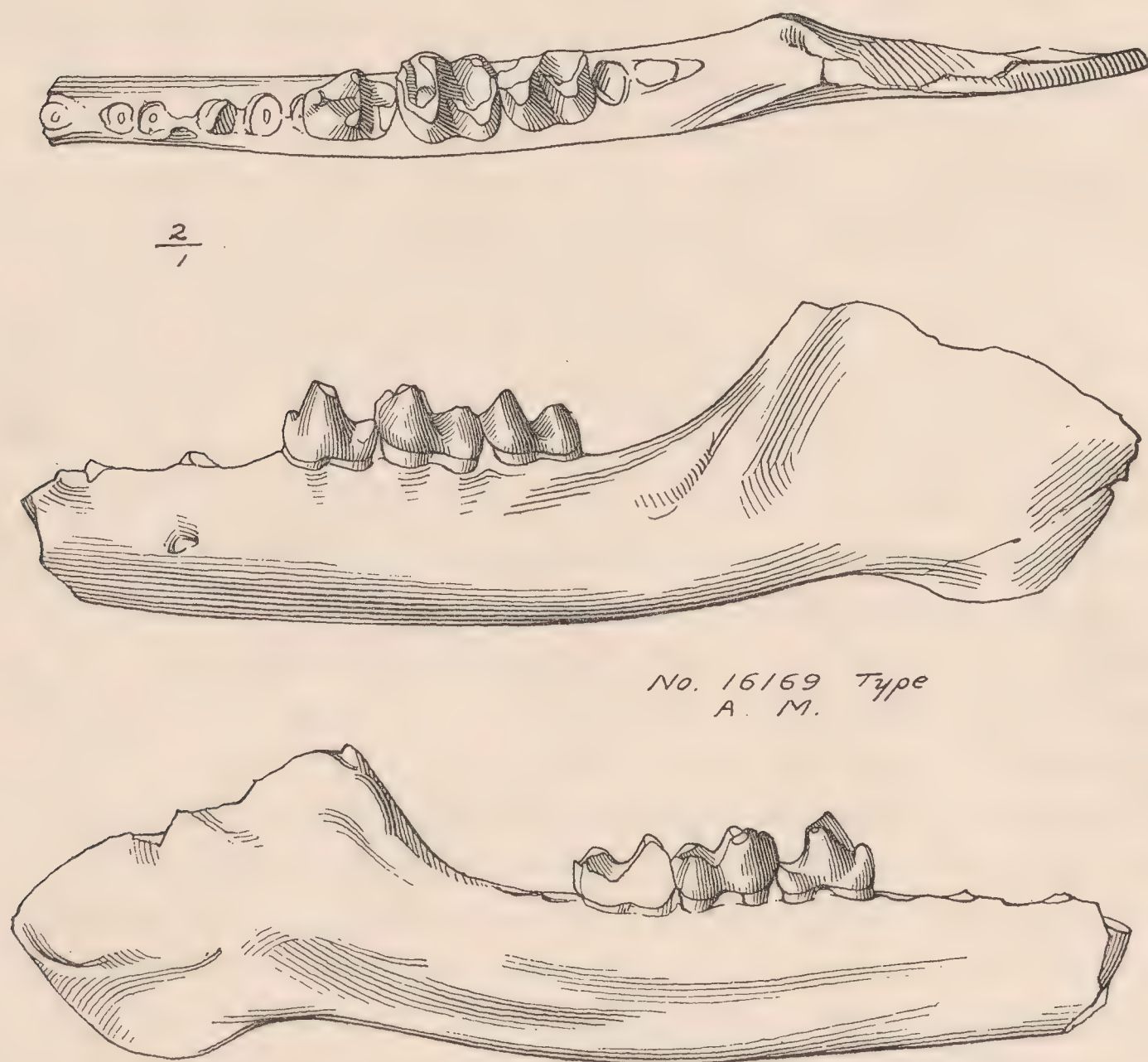


Fig. 35. *Creotarsus lepidus*. Lower jaw of type specimen, crown, outer and inner views, twice natural size. Lower Wasatch, Gray Bull horizon, Bighorn basin, Wyoming.

The lower jaw is perhaps nearer to the insectivore type, especially to the Leptictidæ, than any other, and it is chiefly the peculiar tarsus that makes the ordinal reference of the genus difficult. It is not far outside the range of construction of the tarsus in different groups of Insectivora; but it is not of the characteristic insectivore type, and on this account I am compelled to regard the reference of *Creotarsus* to this order as untenable.

Whatever its ordinal position may be, its affinities with any known mammals appear to be rather distant. It is on this account that it is so

difficult to place. *Apheliscus* has some degree of resemblance, but probably this is rather superficial. Relationships to the Leptictidæ, suggested by the teeth, are not at all confirmed by the tarsal characters.

***Creotarsus lepidus*, new species**

Fig. 35-36

Type.—Amer. Mus. No. 16169, lower jaw, tarsal bones, and other fragments from the lower Gray Bull beds in the Bighorn Basin.

Specific characters.— $P_1-m_3 = 27$ mm.; other characters included in generic description.

Besides the lower jaw the specimen includes calcaneum, astragalus,

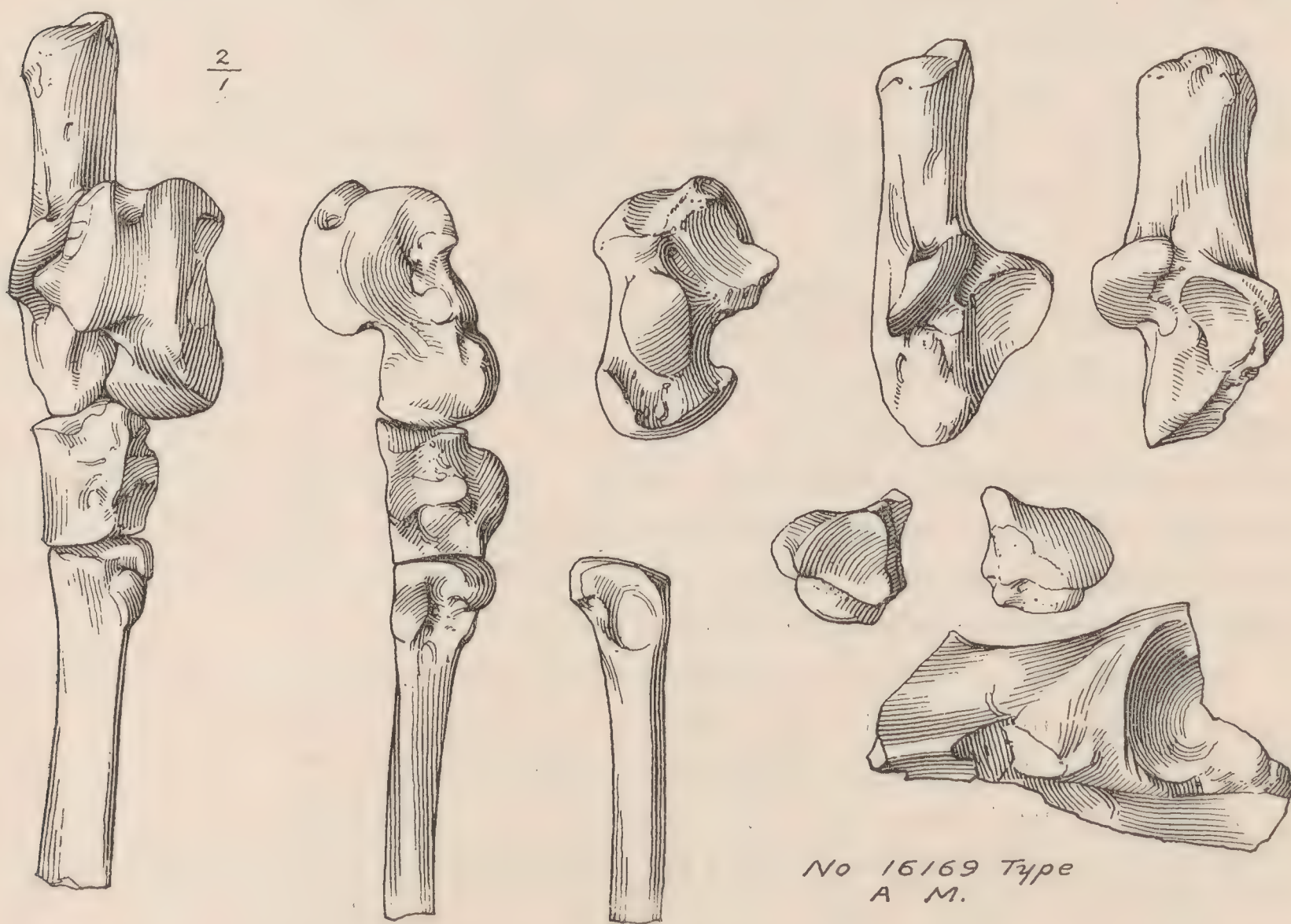


Fig. 36. *Creotarsus lepidus*. Parts of the hind foot and fragment of pelvis. Type specimen, same as Fig. 35, twice natural size. From left to right the figures are (1) dorsal view of astragalus, calcaneum, cuboid, and fourth metatarsal; (2) inner view of astragalus, cuboid and mt.iv; (3) palmar view of astragalus and outer view of mt.iv; (4) dorsal and inner views of calcaneum above, distal and proximal views of cuboid in center, and fragment of pelvis below.

cuboid, most of the fourth metatarsal, two fragments of the proximal end of the femur, and part of pelvis with acetabulum, all found together without association of any other remains, so that there is no reasonable doubt of their pertaining to one individual.

GLIRES (RODENTIA)

Ischyromyidæ Alston, 1876

This order, so numerous and diversified in the later Tertiary faunæ, is represented in the Middle and Lower Eocene by three or more nearly allied genera of a single family. Of these, *Paramys* is the best known. It is also the earliest to appear, and probably represents the primitive type of the Ischyromyidæ. Rodents are unknown in the Paleocene, first appearing in the Sand Coulee level of the Wasatch along with Artiodactyla, Perissodactyla and primates, but are not found in great abundance in the Wasatch faunas. They are all small species of *Paramys*, except for one minute and rare form from the Lost Cabin beds which I have referred to *Mysops*.

The Lower Eocene rodents, so far as known, do not come any nearer to the primitive tritubercular type of dentition than do their successors in the Middle Eocene. The differentiation of the order is evidently of much earlier date than its first appearance in our Tertiary succession.

PARAMYS LEIDY, 1871

Type.—*P. delicatus* Leidy from the Middle Eocene (Bridger) of Wyoming.

Generic characters.—Dentition $\frac{1.0.2.3.}{1.0.1.3.}$. Superior molars tritubercular, hypocone absent or small; lower molars with broad and shallow basin heels, entoconid a distinct cusp, pa^d vestigial or closely connate with metaconid. Incisors typically of moderate width.

The skull and skeleton characters of this genus were fully described in a former article in this Bulletin.¹ The Lower Eocene species are mostly of small size, with low-crowned teeth and marginal cusps. They were revised by Loomis in 1907,² but the true correlation of the horizons was not correctly understood at that time, and the additional material somewhat alters the scope and validity of the species as distinguished by Dr. Loomis.

Paramys major quadratus Loomis

Type.—Amherst Mus. No. 226a, lower jaw from ?Lost Cabin beds of Buffalo Basin, Wyoming.

Specific characters.— $P_4-m_3 = 18$ mm. Otherwise as in *P. major*.

¹ Matthew, 1910. Osteology of *Paramys* and affinities of the Ischyromyidæ. Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 43-71.

² Loomis, 1907. Wasatch and Wind River Rodents. Amer. Jour. Sci., XXIII, pp. 123-130.

The locality as given by the describer indicates that the type is from the upper Wasatch of the Bighorn Valley, probably from the Lost Cabin level, although it may be Lysite. The only specimens in our collections that agree in size are from the Lost Cabin, No. 14718, and Lysite, No. 14722, of the Wind River Basin, both lower jaws; a fragmentary skeleton, No. 15605, from the Lost Cabin of Buffalo Basin appears to be a little smaller, agreeing approximately with Loomis's *P. major* in size. There do not seem to be any constant characters except size to distinguish this species from *P. major*, of which it is very probably merely an advanced mutant.

***Paramys major* Loomis**

Paramys major LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 128, fig. 5; *Plesiarctomys delicatior* COPE, 1881, Bull. U. S. Geol. Geog. Sur. Terrs., VI, p. 184; 1885, Tert. Vert., p. 182, Pl. xxiva, figs. 11-13. Not *P. delicatior* of Leidy.

Type.—Amherst Mus. No. 327a, a lower jaw from Lysite beds of Wind River Basin.

Specific characters.— $P_4-m_3 = 16.5$ mm. Molars robust, cusps marginal, basins broad and shallow.

Thirteen specimens from the Lost Cabin beds and three from the Lysite of the Wind River Basin, twelve from the Lysite of the Bighorn Basin, and two from the upper beds of the New Mexican Wasatch are referable to this species. It is the common species of the Lysite and Lost Cabin. In the Gray Bull horizon it is relatively scarce, although some specimens agree with it so far as comparisons are practicable. It is more robust than *P. copei* and the skeleton parts are uniformly larger; but the construction of the teeth shows no constant distinctions.

***Paramys copei* Loomis**

Paramys copei LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 128; *Plesiarctomys delicatissimus* COPE, 1885, Tert. Vert., p. 179, Pl. xxiva, figs. 1-10. Not *P. delicatissimus* Leidy (*auct.* Loomis).

Synonym.—*P. primævus* Loomis, *bicuspis* Loomis, *loc. cit.*

Type.—Amer. Mus. No. 4755, skull, jaws, and parts of skeleton from Lost Cabin beds of Wind River Basin.

The characters which Dr. Loomis has used to distinguish *P. primævus*, *bicuspis* and *copei* do not appear to be very constant and are so easily obscured by the wear of the teeth that they do not afford any satisfactory separation. There is little but size and robustness of teeth to distinguish *P. major* from this species, and these characters are not wholly constant.

From *P. delicatior* they are distinguished by inferior size, shallower basins, more marginal and smaller cusps, and the surface of the unworn teeth less rugose. *P. delicatissimus* has decidedly larger cusps, deeper and more contracted basins, smaller m_3 , p_4 with anterior cusp narrow and simple.

It is doubtful whether this species is more than a smaller variety or subspecies of *P. major*.

In synonymizing the three species described by Loomis in his paper of 1907, I have given preference to *P. copei* as it rests upon a much more complete type specimen, disregarding page priority for this reason.

To *P. copei* are referred four specimens from the Lost Cabin and two from the Lysite beds of Wyoming, and two from the lower (Almagre) beds of the New Mexican Wasatch. No. 14716 from the Lost Cabin beds consists of teeth and fragmentary skeleton; No. 16299 is a skull and jaws; the others are mostly lower jaws. Twelve jaws from the Gray Bull horizon of the Wasatch are referable to it, but it has not been found in the lowest level.

***Paramys excavatus* Loomis**

Paramys excavatus LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 129, fig. 6.

Type.—Amherst Mus. No. 327, a lower jaw from the Lysite beds of the Wind River Basin.

Specific characters.— $P_4-m_3 = 12$ mm. Cusps small, marginal, basin broad, shallow and smooth.

A lower jaw with probably dp_4 and m_{1-2} from the Lost Cabin beds near Wolton on Alkali Creek in the Wind River Basin is doubtfully referable to this species. No. 15636 and two unnumbered jaws from the Lysite of Fifteen Mile Creek in the Buffalo Basin are more nearly in accord with the type.

Four fragmentary specimens from the Systemodon zone of the Gray Bull and two from the Sand Coulée beds may be provisionally referred to this species, but the reference is based chiefly on size.

***Paramys atwateri* Loomis**

Type.—Amherst Mus. No. 180, a lower jaw with m_{1-2} from the ?Gray Bull beds in the Bighorn Basin.

Specific characters.— $P_4-m_3 = 12.5$ mm., cusps large, basin contracted, metastylid comparatively large.

No. 14724, a lower jaw from the Lost Cabin beds at Davis' ranch on Alkali Creek, Wind River Basin, is provisionally referred to this species.

It is considerably smaller, the teeth measuring only 10 mm. (p_4-m_3), but agrees with *P. atwateri* in the other characters specified by Dr. Loomis. Some of the specimens referred to *P. excavatus* may perhaps pertain to this species.

Paramys buccatus Cope

Plesiarctomys buccatus COPE, 1877, Ext. Vert. New Mex., p. 171, Pl. XLIV, fig. 8; 1885, Tert. Vert., p. 179; (?*Sciuravus*) LOOMIS, 1907, Amer. Jour. Sci., XXIII, p. 130; (*Paramys*) MATTHEW, 1910, Bull. Amer. Mus. Nat. Hist., XXVIII, p. 51.

Type.—U. S. Nat. Mus. No. 1129, upper jaw with p_4-m^2 from Wasatch of New Mexico.

Specific characters.— P_4-m_3 (calculated from the upper teeth of type) = 10 mm. P^4 as large as m^1 .

No topotypes have been found; a jaw from the Lysite with p_4 and alveoli of m_{1-3} , and a jaw from the Sand Coulee beds with p_4-m_3 , agree in size with the type, but are referred only provisionally. The species appears to be scarce. An upper jaw, No. 15710, from the Systemodon zone is of about this size, but does not agree closely with the type. All the above specimens are from the Bighorn and Clark Fork Basins.

Paramys murinus, new species

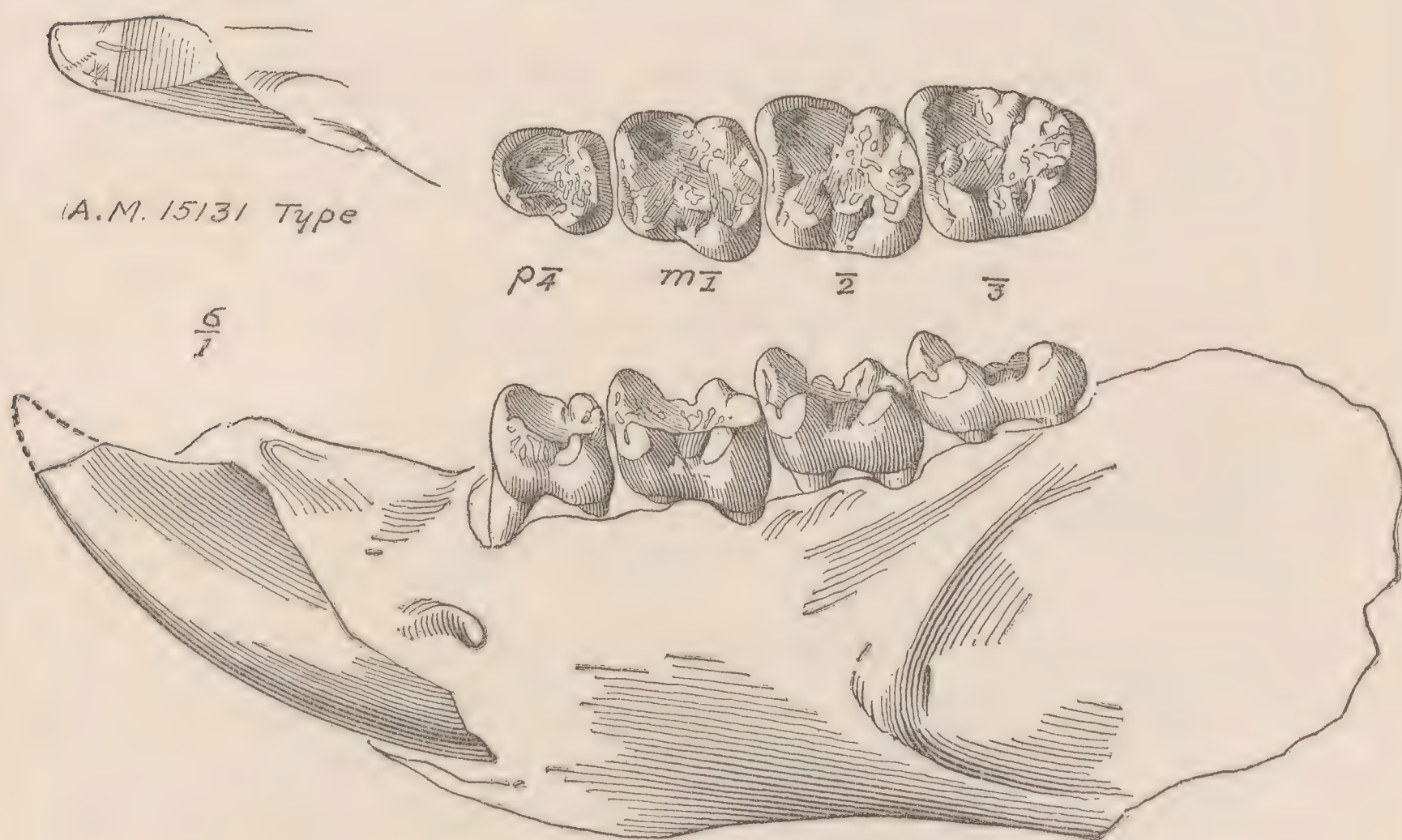


Fig. 37. *Paramys murinus*. Lower jaw of type, external view, and crown view of teeth, left ramus. characters supplemented from the right ramus. Six times natural size. Gray Bull horizon of the Bighorn Wasatch.

Type.—Amer. Mus. No. 15131, lower jaws and part of maxilla from Gray Bull beds of the Wasatch formation, Bighorn Basin, Wyoming.

Specific characters.— $P_4-m_3 = 8.5$ mm. Premolars relatively small, p^3 minute, p^4 much smaller than m^1 ; hypocone of m^1 distinct but much smaller than protocone; protoconid of p_4 small, closely connate on flank of metaconid.¹ Molars longer than wide, heel of m_3 somewhat narrowed. Incisors narrow.

This species differs from *P. buccatus* in its smaller size and reduction of premolars. It is much smaller than any other described species of *Paramys* and agrees with *Sciuravus* in size and in the narrow incisors, but the pattern of the cheek teeth is very different and typically *Paramys*. It probably belongs to the *P. buccatus* group.

MYSOPS LEIDY

Type.—*M. minimus* Leidy, 1873, from the Bridger formation (Middle Eocene) of Wyoming.

Generic characters.—"A smaller animal than *Sciuravus*, with narrower teeth, the upper molars less quadrate, the inner cusps less distinctly separate, the center of the crown more basined. Lower molars narrower, the anterior pair of cusps higher and more crested, the entoconid more central in position. Construction of antorbital region as in *Sciuravus* and *Paramys*."²

The above characterization is based upon referred material of the typical species. I refer provisionally to this genus a species from the Lost Cabin beds which may be structurally ancestral and can hardly be placed in *Paramys*.

Mysops kalicola, new species

Fig. 38

Type.—Amer. Mus. No. 14731, lower jaw with p_4-m_2 from the Lost Cabin beds near Wolton, Alkali Creek, Wind River Basin, Wyoming.

Paratypes.—Nos. 14729, 14730, lower jaws from the same horizon and locality.

Specific characters.— $P_4-m_3 = 6.3$ mm. Lower molars quadrate, with anterior and posterior transverse crests, extero-median cusp, prominent anterior and distinct posterior cingula as in the type species, but the crests lower and less perfected, the crown more flattened than in the type species.

¹ The metaconid or deuteroconid is the principal cusp of p^4 in rodents. See Wortman, 1903, Amer. Jour. Sci., XVI, p. 367.

² Matthew, 1910, Bull. Amer. Mus. Nat. Hist., XXVIII, p. 60.

This species resembles the earlier species of *Paramys* in the low and imperfectly crested cusps and the tendency to form a broad, shallow basin crown with moderate wear.

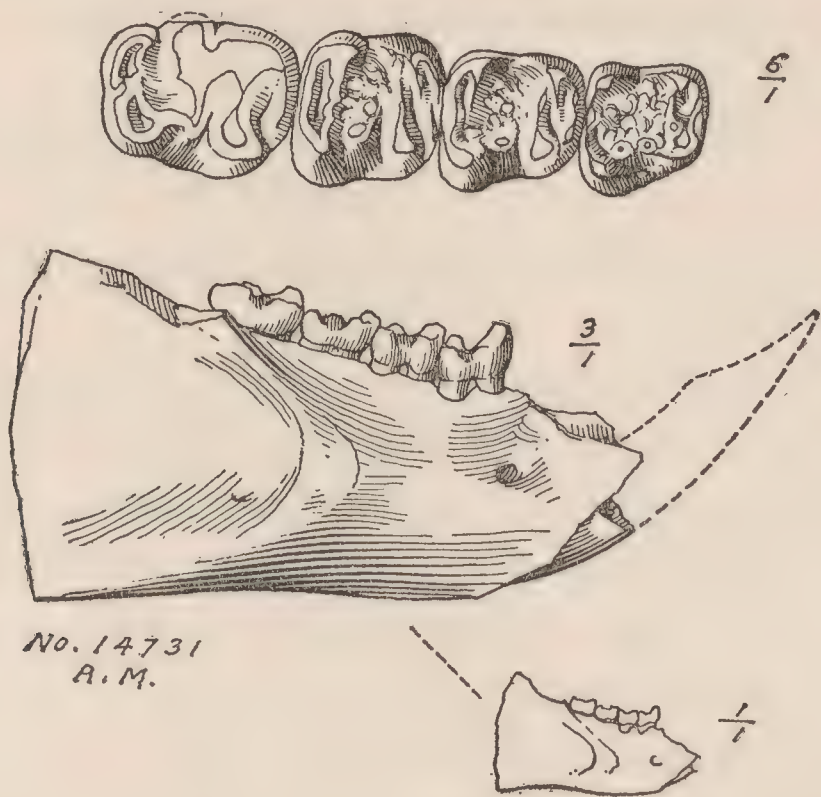


Fig. 38. *Mysops kalicola*. Lower jaw, type specimen, three times natural size; with crown view of molars, six times natural size. The third molar is supplied from the paratype, No. 14729, and is more worn by use than the teeth of the type. From the Lost Cabin zone on Alkali Creek in Wind River basin.

Geological Distribution of *Paramys*, *Mysops* and *Sciuravus* and of the Lower Eocene Species, as Shown by American Museum Specimens

	Sand Coulee	Gray Bull	New Mexican Wasatch	Lysite	Lost Cabin	Bridger	Uinta
<i>Mysops</i>					×	×	
<i>M. kalicola</i>					3		
<i>M. minimus</i>							
<i>Paramys</i>	×	×	×	×	×	×	×
<i>P. quadratus</i>				1	1		
<i>P. major</i>			2	15	13		
<i>P. copei</i>		12	2	2	4		
<i>P. excavatus</i>		?4		3	?		
<i>P. buccatus</i>	?1	?1	×	?1			
<i>P. atwateri</i>		?			?		
<i>P. murinus</i>		1					
<i>Sciuravus</i>						×	×

EDENTATA

PALÆANODONTA, NEW SUBORDER

Ancestral edentates with nomarthrous vertebræ, no ischio-caudal symphysis, canine teeth present and enamel-bearing, no calcified dermal shield, otherwise as in Loricata but less specialized than the Miocene and later members of that group.

Osborn in 1904¹ placed *Metacheiromys* under the Loricata. Its edentate affinities are questioned by Ameghino,² Scott,³ and Winge,⁴ and it apparently represents an aberrant side branch not directly ancestral to the South American Tertiary loricates. It is convenient to rank it for the present in a distinct suborder, whose relations to the Loricata are, I suspect, much like those of the creodonts to the fissipede Carnivora. The only family at present known is the Metacheiromyidæ, which, like the hyænodonts, oxyænids or mesonychids among the Creodonta, is an aberrant side branch, although primitive in most features, and affords important clues as to the derivation and affinities of the Xenarthra and Pholidota.

The Tæniodonta are also, in my opinion, probably an aberrant side branch of the primitive Edentata, and it may be possible in the future to unite the palæanodonts with this group. But at present I see no good evidence for such a step, and, pending a re-examination of the tæniodonts, the present arrangement is less open to objection. The edentate affinities of the Metacheiromyidæ are much clearer than those of the tæniodonts, and they approach nearest to the armadillos, which are regarded by all authorities as the oldest and most primitive group of the undoubted Xenarthra. The tæniodonts were referred by Wortman to the edentates chiefly upon the evidence of resemblances between the stylinodonts and the ground sloths which I think must be explained in large part as convergent, since the sloth group appears to be a derivative of the armadillo group, and there

¹ Osborn, H. F., 1904. An Armadillo from the Middle Eocene (Bridger) of North America. Bull. Amer. Mus. Nat. Hist., XX, pp. 163-165.

² Ameghino, F., 1905. An. Mus. Nac. Buenos Aires, XIII, p. 234. Dr. Ameghino reserves judgment as to its affinities until illustrations are published, regards the presence of large compressed enamelled canines as a "conformation tout-à-fait extraordinaire pour un Edenté primitif," but suggests that it may be related to *Gallixtatus* of the European early Tertiary — which he considers a loricata. This was a rather shrewd guess, not so far from the conclusions reached in this discussion.

³ Scott, W. B., 1913. History of the land mammals of the Western Hemisphere, p. 617. "While these curious animals may very possibly have been referable to the Edentata and at all events had several features suggestive of relationship to that order, it can hardly be maintained that they were unequivocal members of it."

⁴ Winge, Herluf, 1915. Jordfundne og nulevende Gumlere fra Lagoa Santa, p. 307. Dr. Winge concludes that *Metacheiromys* has probably nothing to do with the edentates.

are comparatively few points of affinity between stylinodonts and this more ancient group of the undoubted Xenarthra. The most earnest defender of Wortman's view must admit that there is a good deal of overstatement in his argument, and allow some justice in Winge's recent criticism. But it appears to the present writer that Wortman's critics have gone to the opposite extreme in their views.¹

Metacheiromyidæ Wortman, 1903

Upper and lower canines sharp, compressed, laniary, post-canine teeth reduced or absent, a horny plate probably replacing them. No incisors. Fore and hind feet armadilloid in type, with four or five digits on manus and pes, the lateral digits reduced, the inner possibly vestigial.

The reference of this family to the Edentata was made by Osborn in 1904, upon the basis of two well preserved skeletons of *Metacheiromys*. Owing to the fact that only the preliminary diagnoses of these skeletons have been published, and those without illustrations, the propriety of this reference has been denied. I believe, however, that the publication of the full description and figures will place it beyond reasonable doubt.

In the Gray Bull and Clark Fork horizons of the Wasatch are found species of a more primitive genus of this family. The upper teeth, in *Metacheiromys*, are reduced to one or two vestigial stumps with the exception of the sharp angulate canines. In the new genus they form a series of certainly four, probably six or more, post-canine teeth, represented in our specimens only by alveoli, but of considerable size. The skeleton parts, including the highly characteristic metapodials, are very like the Bridger genus, but less specialized.

PALÆANODON,² NEW GENUS

Type.—*P. ignavus*, new species, from Lower Eocene Gray Bull beds of the Bighorn Basin, Wyoming.

Distinctive characters.—Cheek teeth small, one-rooted, but less reduced than in *Metacheiromys*.

¹ See Wortman, J. L., 1897, Bull. Amer. Mus. Nat. Hist., IX, pp. 59–110, text figs. 1–36.

Ameghino, F., 1905, An. Mus. Nac. Buenos Aires, XIII, pp. 230–234.

Scott, W. B., 1904, Rep. Princ. Exped. Patagonia, V, p. 361.

Gregory, W. K., 1910, Bull. Amer. Mus. Nat. Hist., XXVII, p. 340.

Scott, W. B., 1913, History of the Land Mammals of the Western Hemisphere.

Winge, Herluf, 1915, Jordfundne og nulevende Gumlere fra Lagoa Santa, p. 300.

The affinities of the Tæniodonta can best be determined after the new material from the Paleocene horizons has been described in a revision of the Puerco and Torrejon faunas, shortly to be undertaken by the present writers. Until then, detailed critical consideration of Ameghino's, Scott's and Winge's arguments is postponed.

² Gr. *παλαιος*, ancient; *ἀ*, without; *ὀδόνς* tooth; i. e., ancient edentate.

Palæanodon ignavus, new species

Figs. 39-56, 61-62, 65-68

Type.— Amer. Mus. No. 15086, skull, vertebræ, foot bones, and other fragments of skeleton, from the Systemodon zone of the Wasatch in the Bighorn Basin, Wyoming.

Paratypes.— No. 15698, part of lower jaw; No. 15699, part of lower jaw, ulna, and fragments of humerus and femur; No. 16831, part of lower jaw with several limb and foot bones; No. 15137, fragmentary skeleton, including most of the vertebræ and limb bones and parts of the feet, but no skull parts; No. 15088, limb bones and parts of foot bones; No. 16832, parts of limb and foot bones.

Skull (Figs. 39, 40).— The front and top of the skull are broken and weathered and all parts of the type are partly buried in a hard sandy matrix. The front teeth are not preserved, but on one side of the skull the palate is complete as far forward as the anterior part of the premolar region. Four alveoli are shown, two anterior to the infraorbital foramen, the others behind it. There is no indication of the alveolus of the large caniniform tooth which is so prominent in *Metacheiromys*; if present, this tooth must have been considerably in advance of the four whose alveoli appear. The anterior end of the maxillary-palatine suture is just back of the posterior end of the tooth row. The outer part of the palate is a raised and flattened surface, rugose with irregular longitudinal ridges and grooves, apparently indicating a horny plate; the grooves are more prominent posterior to the tooth row and fade out opposite it, indicating that the plate was thicker posteriorly.

The infraorbital region of the skull is elongate, the cranial region short and wide. The natural brain cast indicates a smooth brain; the inter-orbital constriction is little marked; the occiput is broad and low, the occipital crest sharply defined.

The posterior part of the lower jaw shows a short condyle, somewhat expanded transversely, a small coronoid process and a wide flat angle, not incurved, but ending posteriorly in a prominent spine. The form of the angle is rather more like that of creodonts and primitive insectivores than armadillos. The dentigerous portion of the lower jaw (Fig. 41A) has the same peculiar form as in *Metacheiromys*, a heavy buttress extending along the inner side as far back as the base of the coronoid process, presumably for the support of a horny plate; but the alveoli of the cheek teeth are much larger than in the Bridger genus.

The condyles of the skull are large and wide, the basioccipital broad and flat, but narrowing sharply towards the basisphenoid suture, and the basi-

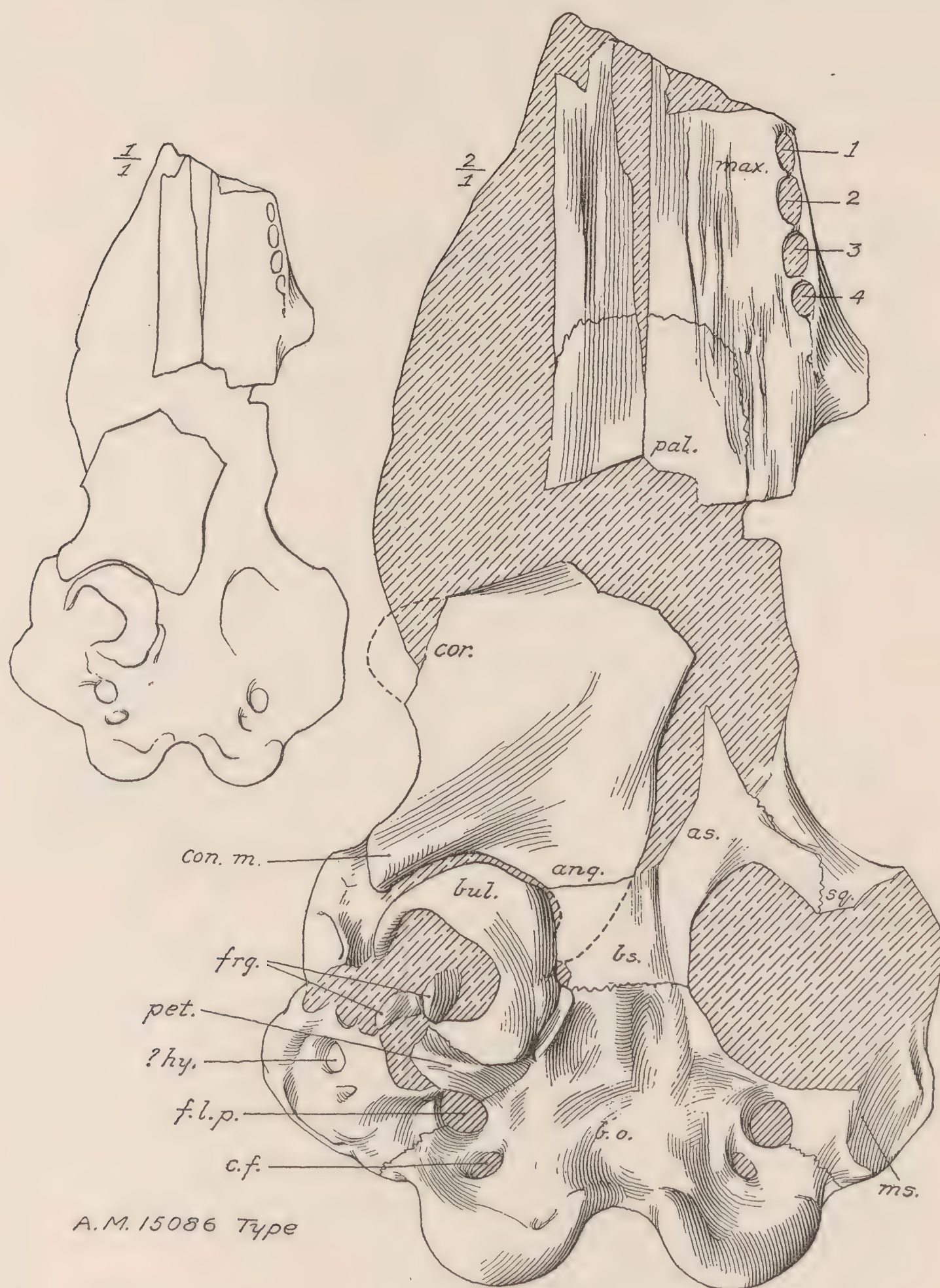


Fig. 39. *Palæanodon ignavus*. Skull of type specimen, twice natural size. Lower Eocene, Big-horn basin, Wyoming. Palatal view, with posterior part of the lower jaw overlying the pterygoid region. 1, 2, 3, 4, alveoli of cheek teeth; *ang.*, angular process of lower jaw (the tip was lost during preparation but had about the form shown in dotted outline); *as.*, alisphenoid bone; *b.o.*, basioccipital; *bs.*, basisphenoid; *bul.*, tympanic bulla (probably composed chiefly of the os bullæ); *c.f.*, condylar foramen; *con.m.*, mandibular condyle; *cor.*, coronoid process of lower jaw; *f.l.p.*, posterior lacerate foramen; *frg.*, fragments possibly of tympanic ring; *hy?*, socket of hyoid arch; *max*, maxilla; *ms*, mastoid; *pal.*, palatine; *pet.*, petrosal crest; *sq.*, squamosal.

sphenoid is comparatively narrow. The space between the condyles and the otic region is considerably greater than in modern armadillos; the mastoid exposure is extensive on the side and base of the skull; it presents large posterior and inferior faces separated by a sharp crest. The condylar

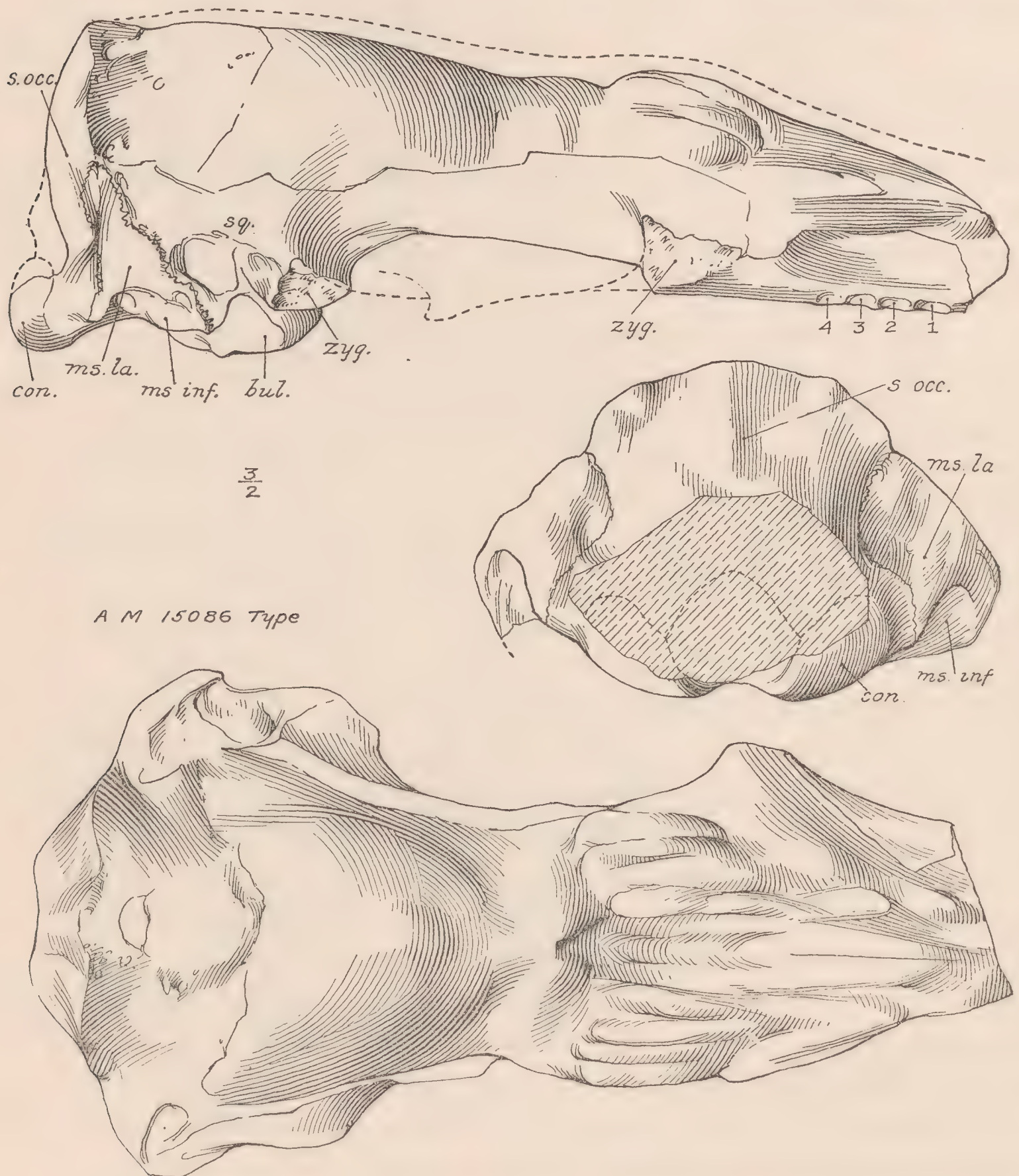


Fig. 40. *Palæanodon ignavus*. Skull of type specimen. Lateral, occipital, and superior views, three halves natural size. 1, 2, 3, 4, sockets of cheek teeth; *bul.*, tympanic bulla; *con.*, occipital condyle; *ms.inf.*, inferior exposure of mastoid; *ms.la.*, lateral exposure of mastoid; *s.occ.*, supraoccipital; *zyg.*, roots of zygomatic arch.

foramen is small and well in advance of the condyles; the posterior lacerate foramen is a little antero-external to it, circular in form as in most primitive placentals, not slit-like as in armadillos or in *Manis*. The tympanic

is expanded into an incomplete bulla supported apparently on the posterior and internal side by ossifications arising from the petrosal, but without any ossified meatus. In the condition of the tympanic region *Palæanodon* appears to be nearest to *Cabassous* among modern forms, but the anterior portion of the tympanic is more expanded, the mastoid exposure much more extensive.

Tatusia has a very narrow mastoid exposure and lacks the supporting plates for the tympanic; *Dasypus* has a completely ossified bulla and bony meatus; so also has the larger species of *Metacheiromys*. *Manis* has a posterior crest on the petrosal that is not a little like *Palæanodon* but the lateral crests of the basioccipital in *Manis* are not present in *Palæanodon*. I cannot be certain whether the sphenoidal wings that extend the posterior nareal channel backwards to the basioccipital in *Manis* are present in *Palæanodon*; there are some doubtful indications of them, but the specimen is somewhat damaged and the hard matrix cannot be safely removed. The well defined occipital crest in *Palæanodon* is a very obvious difference from *Manis*, but there would seem to be a considerable amount of structural correspondence underlying the differences in the cranium.

In several respects the basicranial region of *Palæanodon* approaches the primitive type seen in creodonts and Insectivora. The form and relations of the condylar and posterior lacerate foramina, the extensive exposure of the mastoid and various details of sculpture of the adjacent parts are suggestive of Oxyænidae, Leptictidae and Pantolestidae. They are presumably due to the comparative nearness of all these early Eocene placentals to a common ancestral stock. Modern armadillos have diverged widely both from each other and from *Palæanodon*; the Santa Cruz genera are less diverse, but Scott's figures and descriptions are not very satisfactory for exact comparisons, the specimens being presumably imperfect, so that I have found it better to compare with the modern genera.

If the skull of *Palæanodon* alone were known, one might hesitate to say whether the genus stood nearer fundamentally to the armadillos or to the pangolin, although superficially it is nearer to the former. The skeleton, as will be seen, approaches decidedly nearer to the armadillo type in the structure of the limb bones and of the manus and pes. The vertebræ retain, however, many important characters, for the most part obviously primitive, which are also retained in *Manis*. The characters regarded as primitive are those in which *Palæanodon* resembles the early Tertiary mammals in general, and in particular the Eocene and Paleocene Insectivora and Creodonta. They are not arbitrarily selected in accord with any particular theories of derivation, but are the characters which *Palæanodon* shares with all or most of these primitive placentals, as shown in various well preserved skulls and skeletons which I have studied.

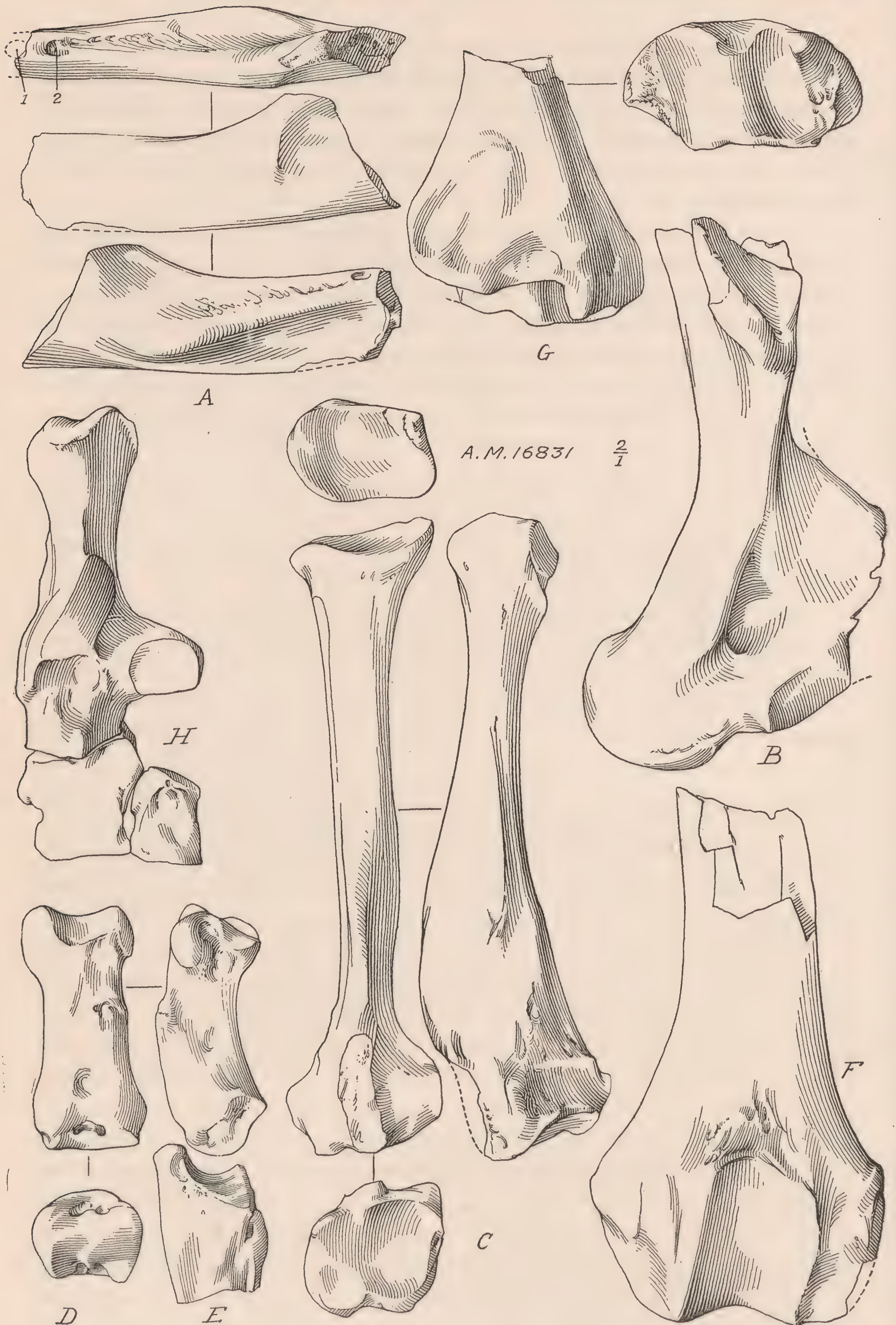


Fig. 41.

Cervical vertebræ (Fig. 42).—The cervicals are preserved in articulation with the skull in the type specimen, but part of the neural arches is weathered away and the remainder buried in such extremely hard matrix that it has not been practicable to clear them up. They are proportioned much as in *Tatusia* or *Manis*, much less shortened than in *Dasypus*. The cervicals are all free, instead of C_{2-4} being united as in the armadillos.

The centra are separate, short and wide and considerably flattened. The vertebrarterial foramen is present except upon the seventh cervical; but the spinal nerves make their exit through a notch in the posterior border of the arch, as in *Manis*, not through separate closed foramina for the upper and lower nerves, as in the modern armadillos. *Palæanodon* and *Manis* retain the primitive condition in this respect, so do the sloths.

The *atlas* is insufficiently exposed to show any very characteristic distinctions.

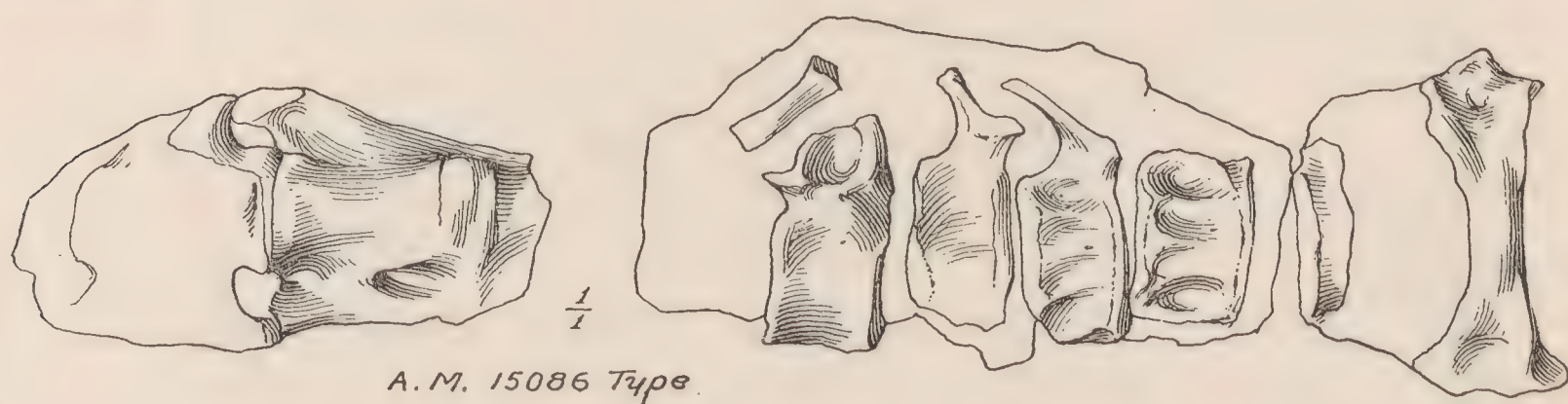


Fig. 42. *Palæanodon ignavus*. Cervical vertebræ and fragment of sacrum, type specimen. Inferior view, natural size.

The *axis* has the anterior part of the spine removed by weathering, but the posterior portion projects strongly backward, overhanging the third cervical, a primitive character retained in *Tatusia*, partly lost in *Manis*, wholly altered in *Dasypus*.

The remaining cervicals have rather slender transverse processes, those of the fourth and fifth strongly projecting backward; the sixth has the usual dependent plate and laterally projecting process; the seventh, a rather slender long process projecting slightly forward. So far as can be judged from the half-buried processes of these vertebræ, they are decidedly more

Fig. 41. *Palæanodon ignavus*. Lower jaw and fragments of skeleton, No. 16831, Lower Eocene, Gray Bull horizon of Wasatch, Bighorn basin. A, part of left lower jaw, superior, external and internal views with alveoli of molar teeth; B, part of humerus, front view, showing deltoid crest and entepicondyle; C, radius, anterior view to left, internal to right, above and below proximal and distal ends; D, third metacarpal, dorsal, inner and distal views; E, ungual phalanx of manus, side view; F, distal end of femur, front view; G, distal end of right tibia, anterior and distal views; H, calcaneum, cuboid, and ectocuneiform, dorsal views. All twice natural size.

like the normal primitive placental type in details than the simplified flattened plates of *Manis* or the short knobby processes of *Dasypus*. Both modern genera have departed far, in diverse directions, from the primitive type which is still largely retained in *Palæanodon*.

Dorsal vertebræ (Fig. 43).—The postcervical vertebræ are not preserved in the type except for a badly weathered portion of the sacrum. In No. 15137 a large number of vertebræ are preserved, sixteen presacral and twenty-seven postsacral, together with the sacrum, pelvis, hind limbs, fragments of the fore limbs, etc. The specimen includes, however, some fragments of a second individual of the same species (besides a few bones of a much smaller mammal and of a lizard) and is therefore unreliable as to the number of vertebræ present in different regions. The anterior dorsals are somewhat smaller than the cervicals; the centra slightly longer but of less

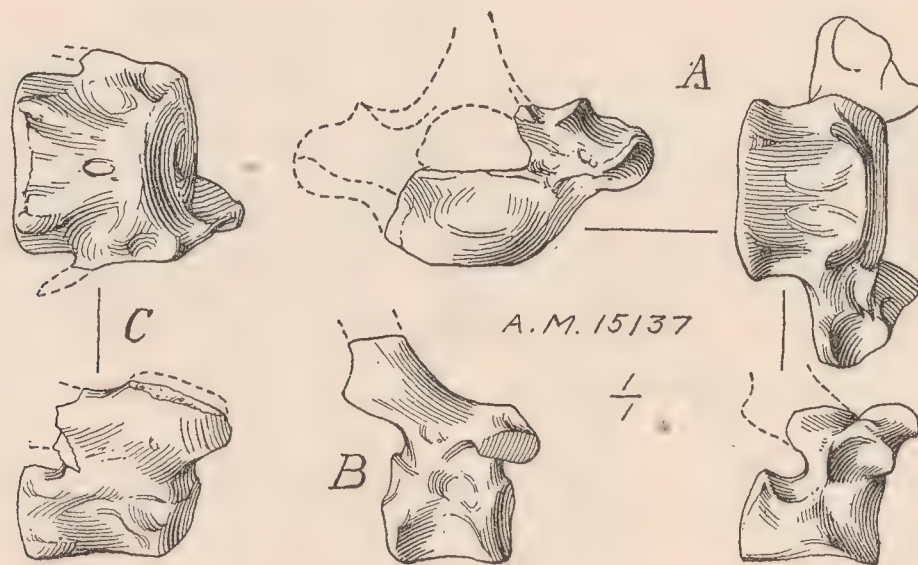


Fig. 43. *Palæanodon ignavus*. Dorsal vertebræ from No. 15137; A, first dorsal, inferior and right side views; B, second dorsal, anterior and right side views; C, posterior dorsal, inferior and right side views. All natural size.

width, much more convex inferiorly. The neural spines are preserved in only one of them, and portions of the arches in others. The first dorsal has the anterior zygapophyses of the usual wide-set cervical type, their articular facets oval and comparatively small but not so small as in *Dasypus*. The tubercular facet is notably large, strongly concave anteroposteriorly and faces downward. The spinal nerve issues through a deep notch, bordered by a sharp rising edge of the centrum behind it. The capitular facet is not concave or sharply defined. Another anterior vertebra, probably the second or third, has part of the neural spine preserved, enough to show that it was of the usual primitive backwardly directed type, trihedral in cross section, much like that of *Dasypus* but less depressed. The zygapophyses also compare with those of *Dasypus*; the centrum has the primitive semi-cylindrical form partly lost in *Manis* by flattening of the under surface, in

Dasypus by excavation of the upper surface. The spinal nerve issues through a notch as in *Manis* but more contracted and more sharply bordered by bony crests.

The posterior dorsals are of larger size, with somewhat broader and more flattened centra, small transverse processes apparently much like those of *Manis*, a deep constricted notch for the spinal nerve; no zygapophyseal facets are preserved on the vertebræ, but they were probably simple and nearly flat, as no other type is indicated among the fragments.

Lumbar vertebræ (Fig. 44).—The centra of four lumbar are preserved, and one with the arch nearly complete. The centra are somewhat longer than in *Manis*, more excavated on the under side and with the median inferior crest much more distinct. The transverse processes are slender, flattened, rise from the anterior end of the centrum, and are directed strongly forward as well as outward. The zygapophyses have large, nearly flat facets, in contrast with the strongly convex facets in *Manis*; the neural spine is apparently short, small, not expanded; the spinal nerves issue through a deep notch with margins more clearly defined than in *Manis*. There is no recognizable foreshadowing of the peculiar “xenarthral” articulations, the spinous zygapophysial process or the reduced transverse process seen in *Dasypus*, the two latter also present in the larger species of *Metacheiromys*; the vertebra differs from that of *Manis* chiefly in retaining primitive characters.

Sacrum (Fig. 48).—There are four sacral vertebræ, the two anterior being the true sacrals. The centrum of the anterior vertebra is like those of the lumbar, those of the two posterior vertebræ are like the caudal centra in type. The neural spines of all four are united into a single crest; the transverse processes of the two anterior are massive, united except for the usual foramina at the base for exit of the nerves, and expanded distally for sutural union with the ilium. The two posterior sacrals have their transverse processes united into a thin, flat, broad plate, perforated at the base for exit of the spinal nerves, its lateral margin approaching the superior border of the ilium but not united to it at the anterior end as it is in *Dasypus* and *Manis*. The anterior zygapophyseal facets are large, wide apart, face upward, and are but slightly concave.

Caudal vertebræ (Fig. 45).—The caudals are of large size and numerous,

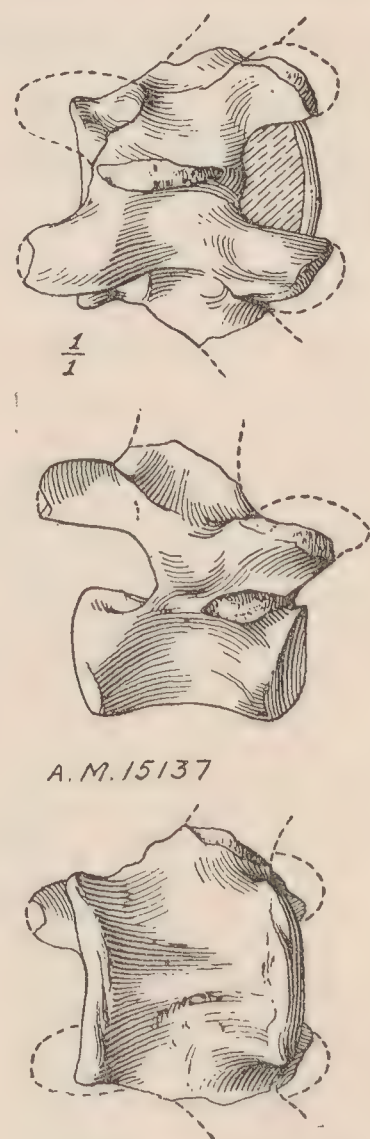


Fig. 44. *Palæanodon ignavus*. Lumbar vertebra from No. 15137. Superior right side, and inferior views, natural size.

and the tail was evidently long and heavy, comparing more nearly with *Manis* in relative size, and with *Dasypus*, less closely with *Tatusia*, in the structure of arches and transverse processes; the chevrons, however, are like those of *Tatusia* or of *Manis* but very unlike those of *Dasypus*. The anterior caudals have moderately long centra, comparable with the coössified caudals that constitute the posterior part of the sacrum of *Dasypus*, but with transverse processes of less width — wider than those of the first free caudals in *Dasypus* — and not united to the ischium nor, so far as known, to each other. Their zygapophyses are of moderate size, further apart than in *Dasypus*, not so far as in *Manis*, with slight curvature of the facets. In the anterior median caudals the zygapophyses are much reduced, and both these and the transverse processes appear to be much like the anterior free caudals of *Dasypus* except for the greater length of the centra

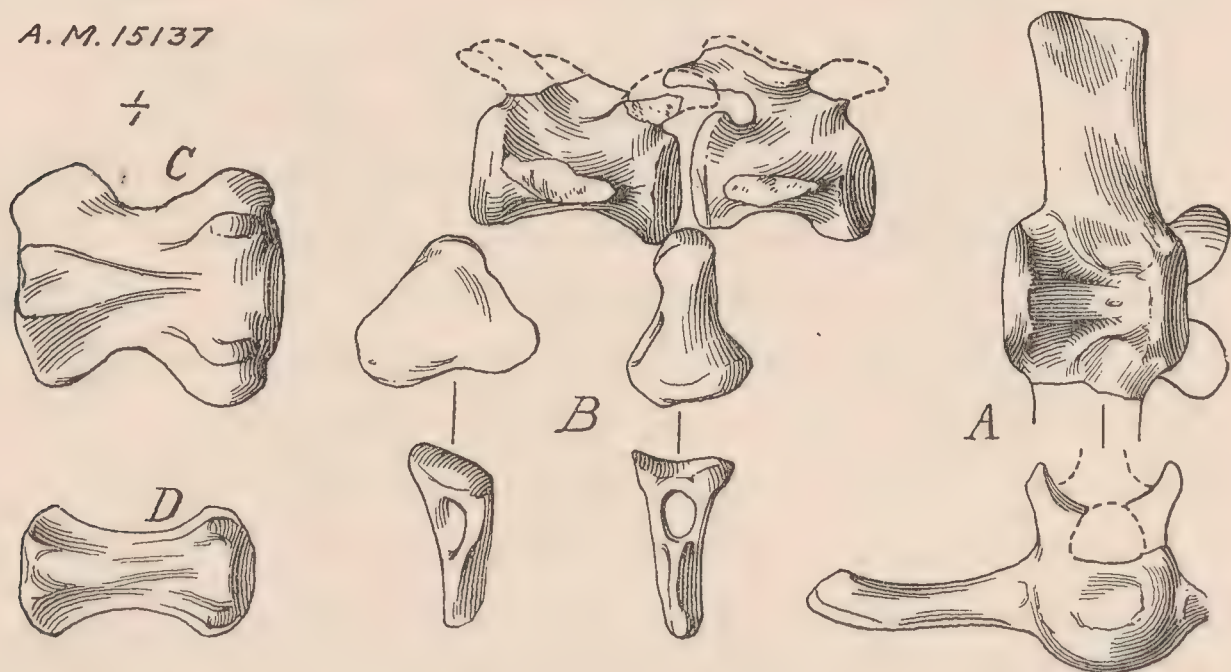


Fig. 45. *Palæanodon ignavus*. Caudal vertebræ from No. 15137; A, proximal caudal, inferior and anterior views; B, anterior caudals, right side views with chevrons in position, and anterior views of chevrons; C, median caudal; D, distal caudal, superior views. All natural size.

and the widely different type of chevron, which is very like that of *Tatusia*, differing from *Manis* chiefly in that the hæmal canal is (as in *Dasypus*) very much smaller. In *Dasypus* the inferior ends of the chevron bones are divergent and expanded for support of the tail-sheath.

The posterior median caudals have the zygapophyses and neural arch progressively reduced, the transverse processes changed in type, reduced in length and expanded anteroposteriorly to a horizontal plate, much as in the corresponding region of the tail in *Dasypus*; the vertebræ are of larger size throughout.

The distal caudals maintain their length but decrease in size, and the transverse plates and neural arches are progressively reduced, much after

the fashion of *Dasypus* save as to size. But, so far as can be judged, the tail must have been nearly as long and robust as in *Manis*; the caudals of *Manis*, however, maintain almost to the tip of the tail the same type of transverse process as in the anterior portion. In *Tatusia* the tail is perhaps somewhat longer than in *Dasypus*, but the ends of all the caudal transverse processes are expanded and modified for support of the tail-sheath.

The fore limb.—In the type specimen, No. 15086, the distal half of one radius, the distal end of the other, a ?cuneiform, one complete and one incomplete metacarpal represent the fore limb. In Nos. 15137 and 16831 some parts of the fore limb bones are preserved; but they are best shown in No. 15088, a partial skeleton, chiefly fore and hind limb bones.

Humerus (Figs. 41B, 61B).—The right and left humeri are preserved in No. 15088 but both, unfortunately, lack the proximal end. No. 16832 includes a humerus with the proximal end complete. The bone is nearly as large as in *Dasypus*, and like it in most features; the deltoid crest is prominent, broad and flattened, ending abruptly distally, but it is directed anteriorly instead of anteroexternally, and the external margin is continued proximally as a prominent crest instead of fading out toward the head as in *Dasypus*. The construction and proportions of the trochlea and entepicondylar foramen are very much alike in the two genera; the supinator crest is more prominent in *Palæanodon*, the inner epitrochlean process less massive. In *Manis* the deltoid process is reduced to a single crest, which is less prominent but continues down nearly to the entepicondylar bridge; the supinator crest is much reduced, the trochlea is of less width and greater depth.

The *ulna and radius* (Figs. 41C, 46, 62) are somewhat longer in the shaft than in *Dasypus*, and less massively proportioned. The olecranon lacks the peculiar inward twist of *Dasypus* but is like that of *Tatusia*; it is fully as long, extends directly in line with the shaft, and is transversely expanded toward the tip by inner and outer crests. The humeral articulation is less expanded than in *Dasypus*, but its margins are damaged so that its complete form is not seen. The upper part of the ulnar shaft is as wide and as deep as in *Dasypus*; distally it contracts in width instead of expanding, and the cuneiform articulation is much smaller than in the modern form and strongly oblique, facing more internad than distad. The radius has, like the ulna, a smaller humeral

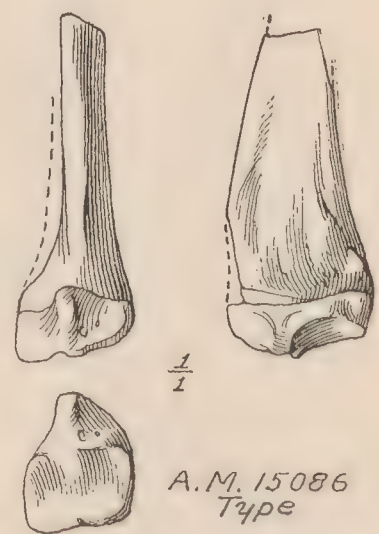


Fig. 46. *Palæanodon ignavus*, type specimen, distal half of radius, anterior, external and distal views, natural size.

articulation than in *Dasypus*, being less extended transversely; the proximal portion of its shaft has about the same proportions, but distally it is more enlarged, the characteristic anterior crest being more prominent and continuous than in the modern armadillos, and the distal facets for scaphoid and lunar much larger, facing more distally, and distinct from each other. The prominent styloid and anterior processes at the distal end of the radius of *Dasypus* are lacking in *Palæanodon*.

In *Manis* the olecranon is much shorter, the ulnar shaft is not so broad, the head of the radius is larger but less expanded transversely, the anterior crest of the distal part of the radius is less prominent; the distal articulations of radius and ulna are very much the same as in *Palæanodon* and *Metacheiromys*.

The fore limb bones are very near to those of *Metacheiromys* in all details of construction. In the humerus the deltoid crest does not extend so far down and the supinator crest appears to be less expanded; in both these features *Palæanodon* is nearer to *Dasypus* than is *Metacheiromys*. The radius differs from that of the Bridger genus in the distal articulation, the facets for scaphoid and lunar being indistinguishable in *Metacheiromys*. The shaft of the ulna is broader and flatter in *Palæanodon*, which, in this respect also, comes nearer to the modern armadillos. The olecranon of *Metacheiromys dasypus* is quite different from that of *Palæanodon* and like that of the modern *Dasypus*; in the small *M. tatusia* it is like *Palæanodon* and the modern *Tatusia*.

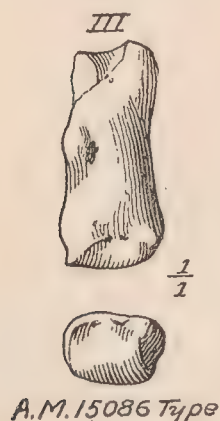
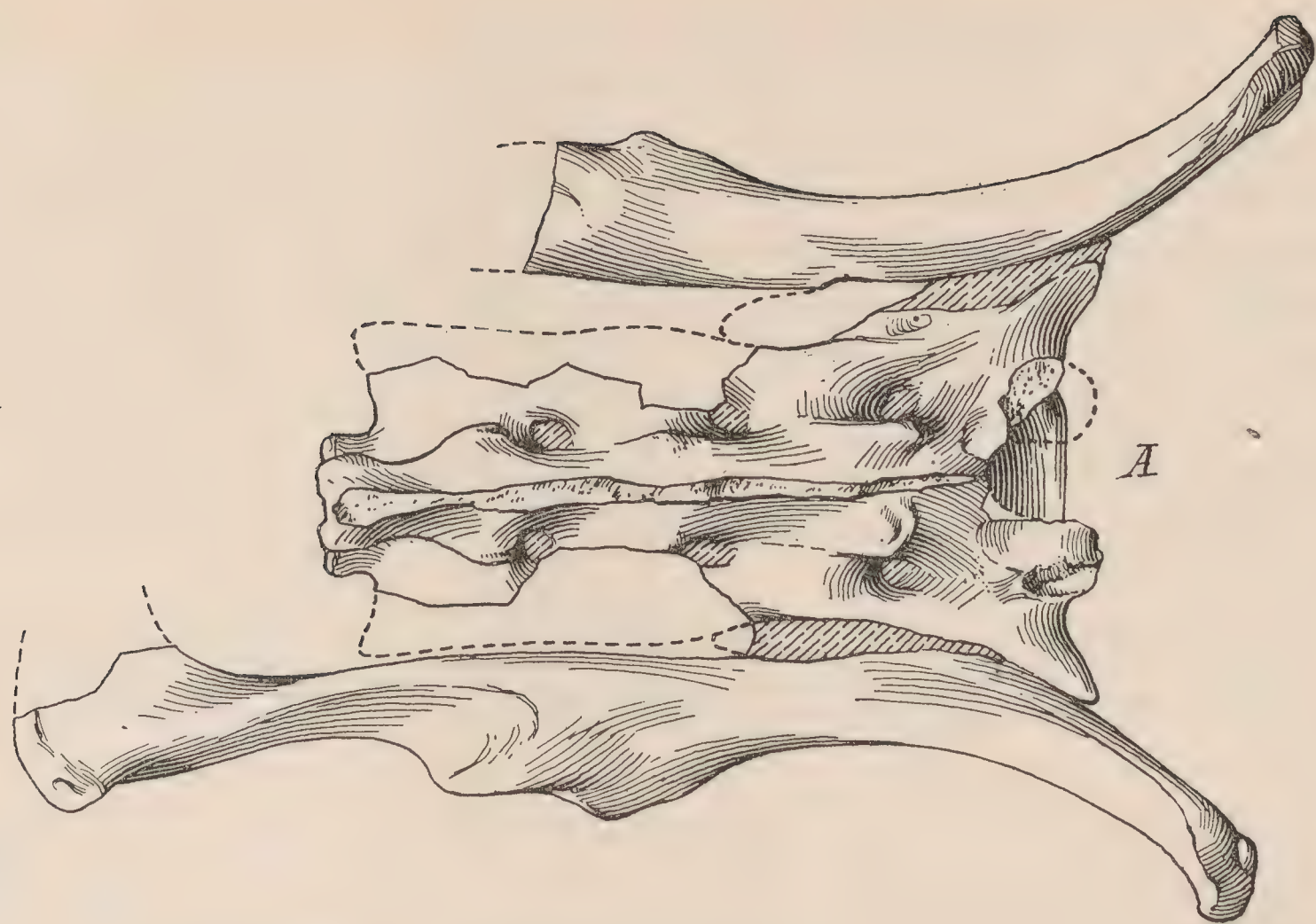


Fig. 47. *Palæanodon ignavus*. Third metacarpal of type specimen. Anterior and distal views, natural size.

Manus (Figs. 41 D and E, 47; compare also figs. 57–60, 64).—Of the carpus no recognizable bones are preserved except the cuneiform in the type, which, so far as can be seen, is very much like that of *Manis*. One complete metacarpal, the third of the right side, and another damaged mc. II? are preserved in the type. Mc. III is a rather short stout bone, but longer and less specialized than in *Metacheiromys*. The diaclasts are much less developed than in *Dasypus*, and the distal

articulation, while evidently on the way to assume the peculiar form characteristic of *Metacheiromys* and of the armadillos, has retained a good deal more of the primitive normal type. The dorsal process at the internal side of the middle of the shaft is distinct, but less prominent than in *Metacheiromys*. In *Dasypus* it is nearer to the proximal end of the shaft.

The supposed mc. II is considerably shorter than mc. III and appears to be somewhat smaller in the shaft; its distal end is weathered and it is incased in very hard matrix so that it cannot be fully examined.



A. M. 15137

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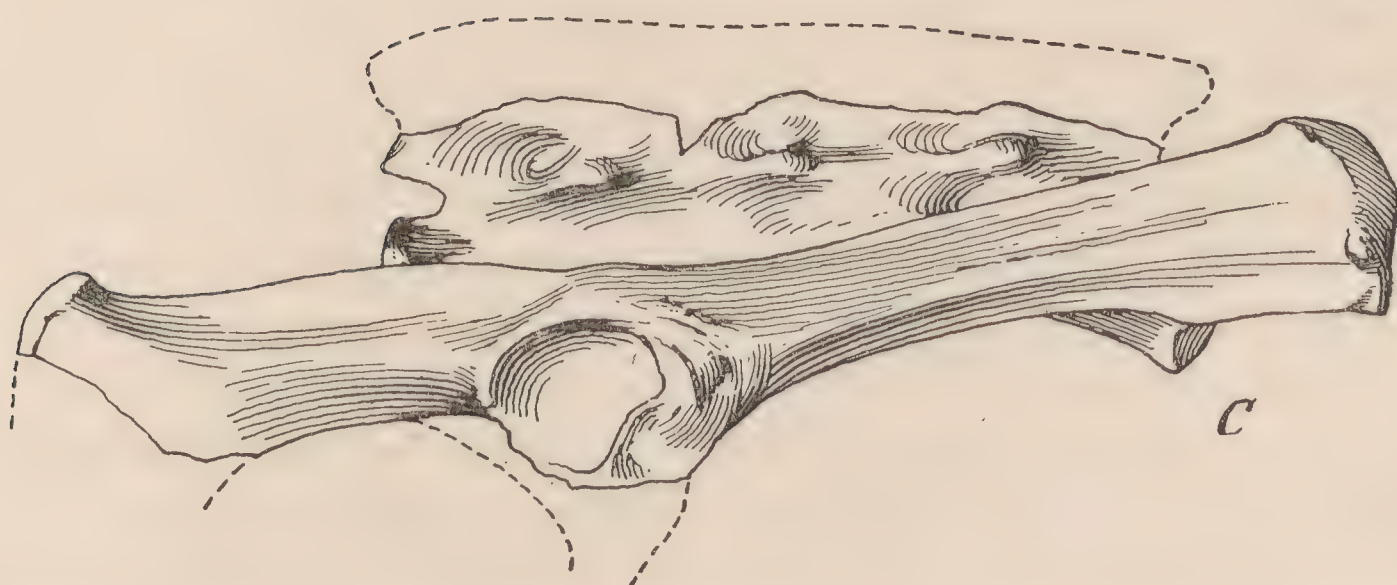
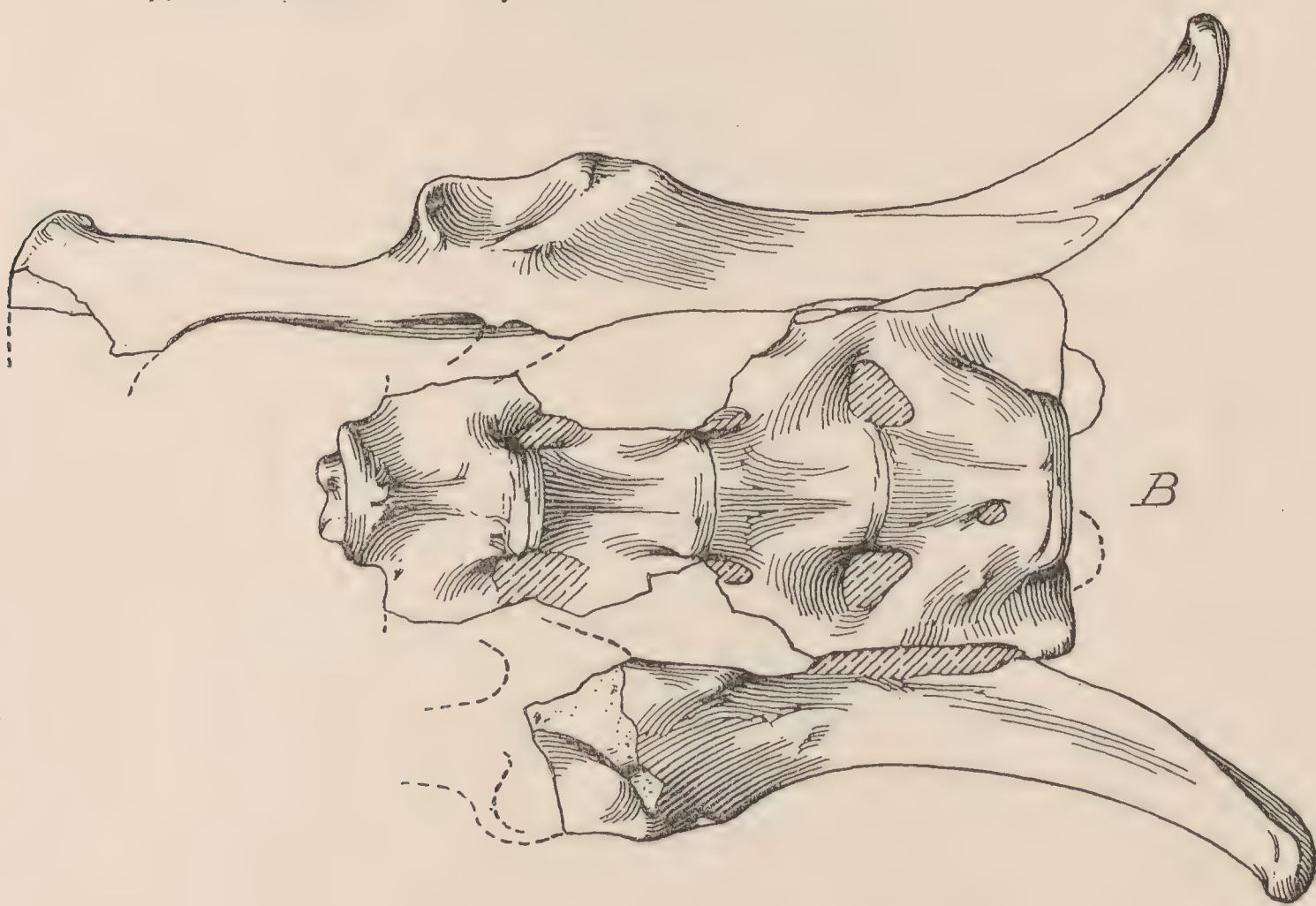


Fig. 48. *Palæanodon ignavus*, No. 15137. Pelvis and sacrum, superior, inferior, and right lateral views, natural size.

Manis has metacarpals of a different type; short and stout, with very prominent high median keels at the distal end, very like those of the sloths, especially the Miocene sloths, but quite unlike those of the armadillos. *Palæanodon* and *Metacheiromys* are decidedly nearer to the armadillos in this respect, although more primitive; but it should be observed that the peculiar articulations of *Manis* may well be considered as derived from the metacheiromyid type, just as the similar sloth articulation is a derivative of the primitive armadillo type.

The phalanges of the first and second row in the manus are broader and longer than in *Metacheiromys*, otherwise very similar. They are much

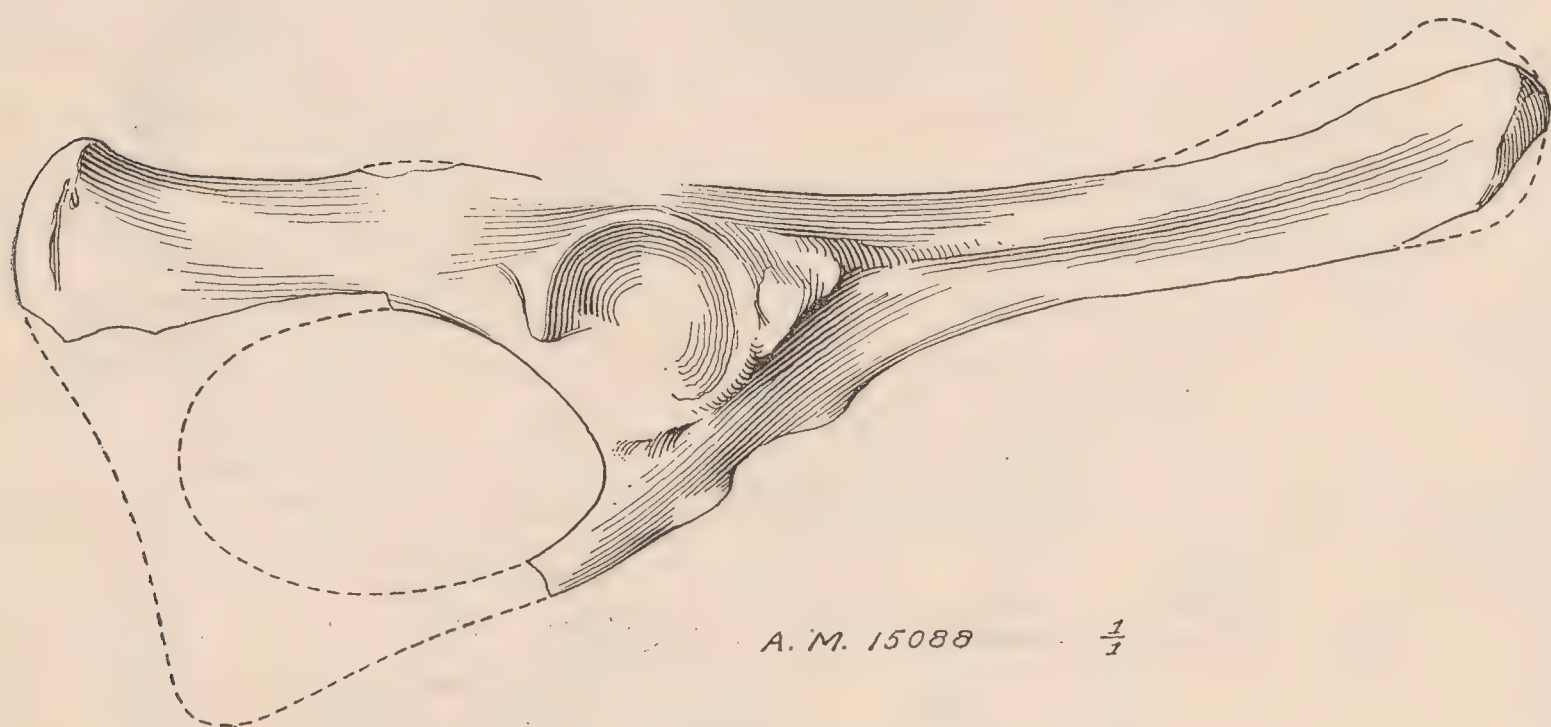


Fig. 49. *Palæanodon ignavus*, No. 15088. Pelvis, right side view, natural size.

less shortened and specialized than in *Dasypus*, but quite similar to those of *Tatusia*. The ungual phalanges are large, compressed, unfissured, quite similar to those of *Metacheiromys*. They are higher and more compressed than the unguals of the armadillos, very like those of *Hapalops* and other primitive ground-sloths, except for the smaller size. They are quite unlike the long and very deeply fissured, but not compressed, unguals of *Manis*.

Pelvis and Hind Limb.—The pelvis (Figs. 48–49) is preserved in No. 15137, No. 15088, and a part of the ilium in the type specimen No. 15086. Fragments of the pelvis are also included in other fragmentary specimens, but the characters are drawn from the two first mentioned individuals.

The ilium is a long trihedral rod, considerably but not abruptly everted, flattened towards the tip into a thick vertical plate, but not notably expanded. The sacral articulation occupies the entire width of the middle third of the ilium; the external crest is obscure and not at all sharp, in

contrast to *Dasypus* or *Tatusia*; the eversion of the tip is intermediate between these two genera.

The ischium is a long straight rod continuing backward in a direct line with the ilium; it is more flattened and only two-thirds as long. The superior crest, which in the armadillos unites with the transverse processes of the posterior sacro-caudal vertebræ, is in *Palæanodon* quite rudimentary, and limited to the middle portion of the shaft. In *Metacheiromys* it is more advanced. The distal end of the ischium is broadened and twisted so as to throw the upper point outward.

The pubis has the characteristic edentate type of a long slender rod, arising from below the anterior part of the acetabulum and extending almost as much downward as backward, so as to inclose an exceptionally large obturator foramen. This is the xenarthral type; the pelvis of *Manis* is quite different, the pubis being shorter, flatter, arising from beneath the posterior side of the acetabulum, the obturator foramen small, the pelvis considerably shorter, with only a ligamentous union between ischium and caudals. In *Metacheiromys* the ischium is shorter and the crest along its superior border is more developed; otherwise there is little difference from *Palæanodon*.

The *femur* (Figs. 41 F, 50–52, 65) is of moderate length, not unlike that of *Dasypus*, but longer and heavier and somewhat less flattened distally. The head is not so sessile, the great trochanter is wider and farther apart from the head, but of less depth; the lesser trochanter does not extend up so close to the head; the digital fossa is broad and deep; the third trochanter is somewhat less prominent and stands relatively further up on the shaft than in *Dasypus*. The patellar trochlea is a little narrower and longer, is set nearly median instead of being nearer the external side, and directs rather towards the head of the femur than towards the great trochanter as it does in *Dasypus*. In *Tatusia* the femur is larger, with high massive greater trochanter; the lesser trochanter has more the form of *Palæanodon*; the third trochanter is lower down on the shaft and more prominent; the distal end of the *Tatusia* femur is somewhat deeper antero-posteriorly than in *Palæanodon*, but the direction and position of the patellar groove is much as in *Dasypus*. The marked ridge of the front of the femoral shaft in *Tatusia* is quite rudimentary in *Palæanodon*.

The *tibia* (Figs. 41 G, 53–54, 66 B; compare also fig. 57) is about as heavy as in *Dasypus* but a fifth longer, suturally united with the fibula at the lower end, but with a circular, flat, distally facing fibular facet at the upper end. The cnemial crest is hardly as heavy and continuous as it is in *Dasypus* and *Tatusia*, but of similar type. The distal end is also of similar general type to that of *Dasypus*, but not so wide, of slightly greater antero-

posterior depth, with somewhat heavier internal malleolus and the fibular articulation for the astragalus definitely confined to the external side of its outer trochlean crest. *Tatusia* has a larger tibia-fibula, the consolidation more advanced; further stages in this union are seen in the glyptodonts.

The hind limb bones compare rather closely throughout with those of *Metacheiromys* in details of construction. The femur of the Bridger genus is nearer to that of *Dasypus* in the more flattened shaft and broader distal end, the broader and shorter trochlea, somewhat

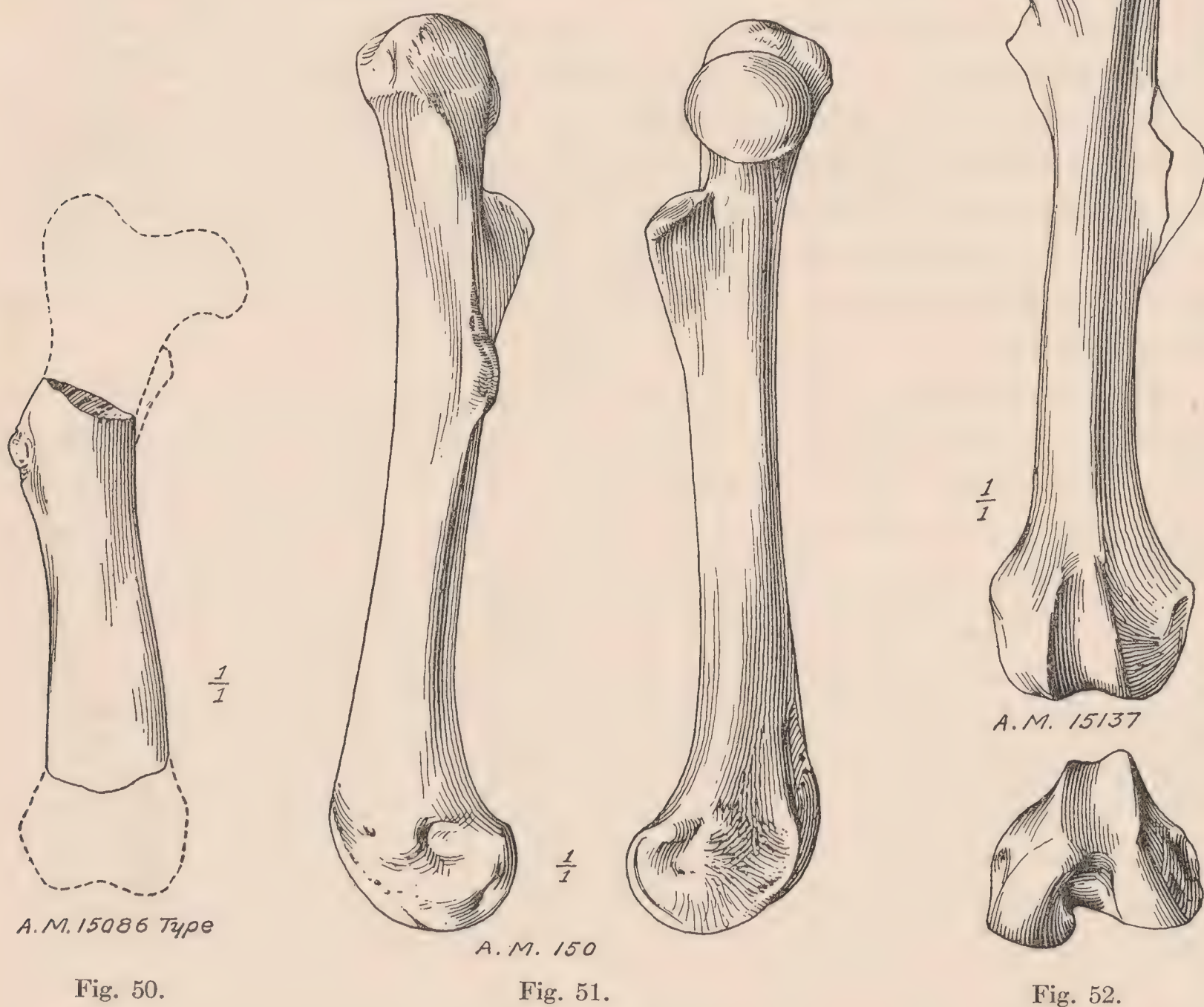


Fig. 50. *Palæanodon ignavus*, type specimen. Part of femur, the ends restored in dotted outline from No. 15088. Front view, natural size.

Fig. 51. *Palæanodon ignavus*. Femur of No. 15088. (No. 150 in error on figure). Internal and external views, natural size.

Fig. 52. *Palæanodon ignavus*. Femur of No. 15137. Proximal, anterior, and distal views, natural size.

higher position of the third trochanter, etc.; the tibia also is somewhat more like that of *Dasypus*.

Manis differs rather widely in the structure of the hind limb bones.

The great trochanter of the femur is reduced so that the head considerably overtops it, the digital fossa has disappeared, the lesser trochanter is a rounded knob instead of a flattened prominent crest, the third trochanter has wholly disappeared; the patellar trochlea is very wide, short and flat. The tibia has wholly lost its cnemial crest and is separate from the fibula at either end. The constructional peculiarities of the hind limb bones in *Manis* are largely analogous to those of the *Gravigrada*, an analogy which, as will be seen, is more marked in the foot bones and extends to other parts of the skeleton as well.

The Hind Foot (Figs. 41 H, 55-56, 67-68; compare also figs. 57 and 60).—In the type of *P. ignavus* a part of the hind foot is preserved, consisting of metatarsals II-V, more or less imperfect but nearly in articulation and with some of the phalanges attached. In No. 15088 the astragalus, lacking the head, and a few phalanges and parts of metapodials are present; in No. 15137 the principal tarsal bones, parts of metatarsals, and a few phalanges; and various other specimens include complete hind foot bones mostly unassociated.

The astragalus has a moderately wide body with trochlea about as deep as in the armadillos but not nearly so short anteroposteriorly. The trochlea is bounded by two symmetric keels, and the fibular facet is more vertical than in *Dasy-*
pus. There is no astragalar foramen. The head is of flattened oval form, not unlike *Dasypus* except that it is hardly as sessile. The sustentacular facet is circular and distinct, the astragalo-calcaneal facet rather broad and shallow, widest behind, both being much as in *Dasypus*.

The calcaneum has a shorter body than in *Dasypus*, the tubercalcis is slightly longer and deeper but not so wide toward its outer end, the peroneal tubercle is somewhat less prominent.

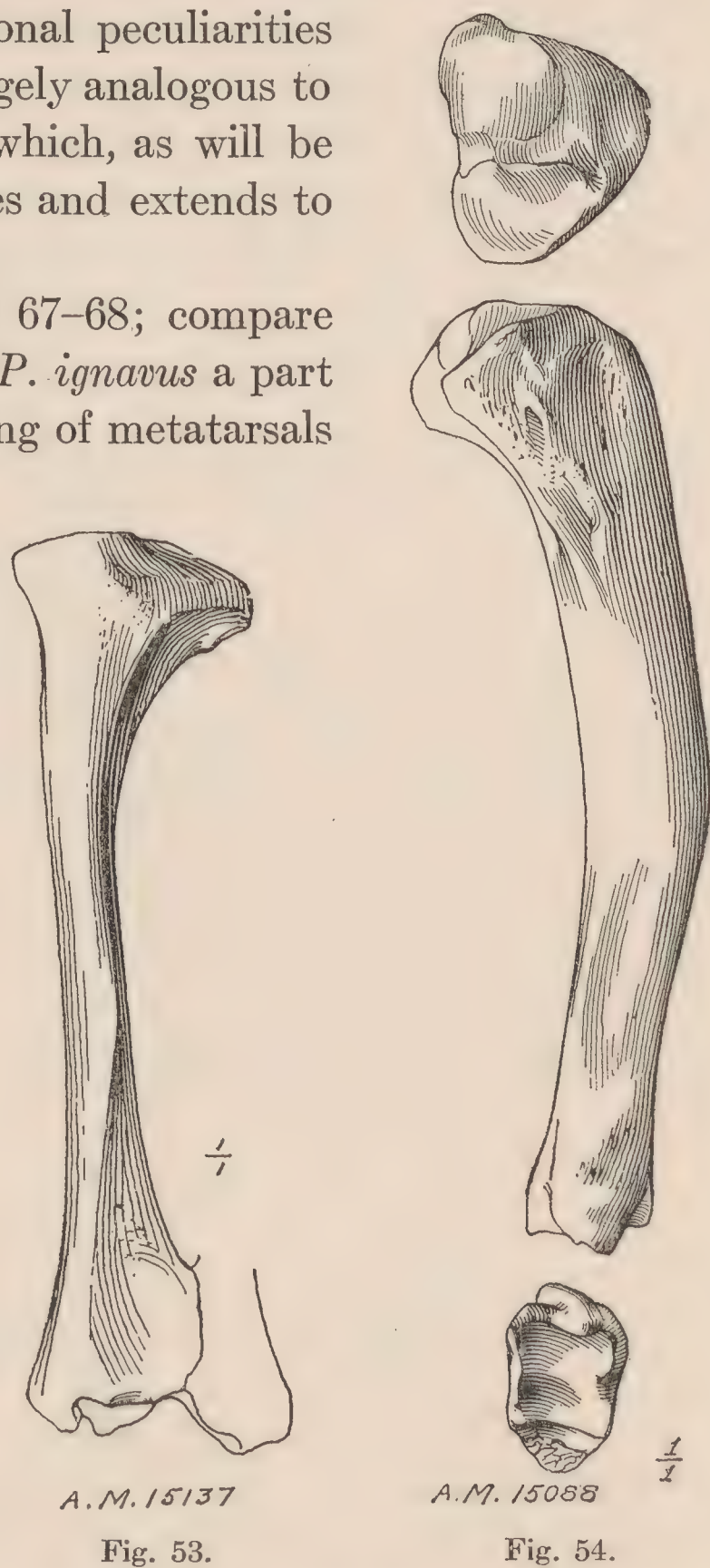


Fig. 53. *Palæanodon ignavus*. Tibia of No. 15137. Anterior view, natural size.

Fig. 54. *Palæanodon ignavus*. Tibia of No. 15088. Proximal internal and distal views, natural size.

The navicular has a heavy inferior hook, but not so large as in *Dasypus*. The facet for the ectocuneiform is wider but not so deep; the mesocuneiform facet is convex rather than concave, somewhat wider than in *Dasypus* but not nearly so deep dorso-palmar, and the entocuneiform facet is quite small, strongly convex, and faces ento-distad, instead of being flat and facing internally as it does in *Dasypus*. This conforms with the greater reduction of the internal digit in the Metacheiromyidæ.

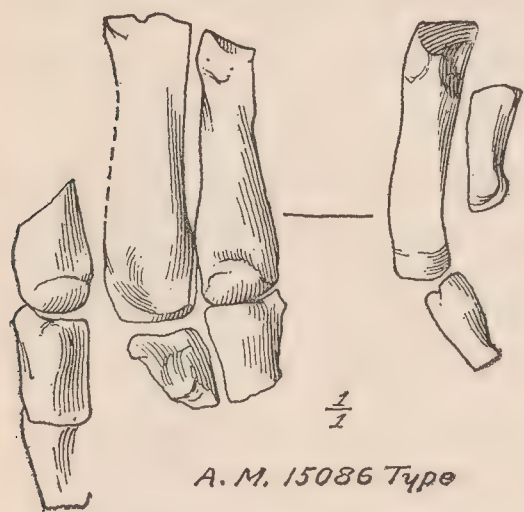


Fig. 55. *Palæanodon ignavus*, type specimen. Part of hind foot, dorsal and internal views, natural size.

Of the four metatarsals in the type, only the distal end of mt. IV is preserved. It is about as robust as in *Dasypus*. The entire length of the others is preserved. The second and third are about four-fifths as long as in *Dasypus*, the second considerably slenderer and less expanded proximally. The first metatarsal is greatly reduced, as in *Dasypus*, but is about three-fourths as long with a considerably heavier shaft. The distal ends of all these metatarsals are more primitive than in *Dasypus*, although they show the armadilloid type of specialization in a rather rudimentary stage; but their precise form in the type has been largely obliterated by weathering or unskilful preparation. In other specimens the metatarsal facets retain part of their primitive convexity from side to side on the dorsal portion; the median keel on the palmar side of the facet is limited and similar in type to that of *Dasypus*,

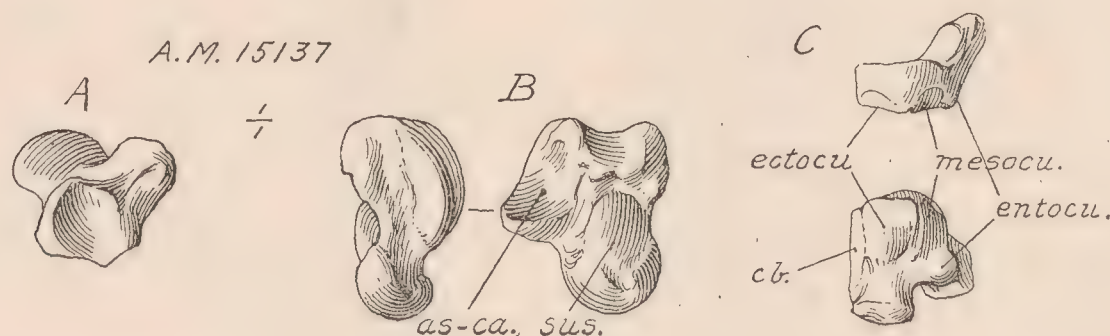


Fig. 56. *Palæanodon ignavus*. Tarsal bones of No. 15137; A, distal view of calcaneum; B, internal and inferior views of astragalus; C, superior and distal views of navicular. All natural size.

but the lateral ledges are less sharp or prominent. There is nevertheless a distinct tendency to excavation of these facets in the palmar face on each side of the median keel, a character much more marked in the metacarpals and very characteristic of the Loricata.

The phalanges of the pes in *Palæanodon* are somewhat shorter than in *Dasypus*, and somewhat flatter. The distal facets of the first series are not reflected over the dorsal surface of the bone as they are in *Dasypus*, but

face only distad and palmad. The proximal facets of the phalanges of the second row are correspondingly limited. This is a primitive character found in many Paleocene and early Eocene mammals. The ungual phalanges attributed to the pes are much like the corresponding bones of *Dasypus*, and differ from those of the manus in their small size and uncompressed subtriangular form.

The pes of *Tatusia*, as compared with *Dasypus*, has some nominal points of resemblance to that of *Palæanodon* but none that appear to me significant. The tuber calcis is deep and narrow, but of peculiar type; the metapodials, especially the lateral pair, are short and massive and the phalanges very short in comparison with those of *Dasypus*, but there is nothing that adds to the evidence as to the relationships of *Palæanodon*.

The pes of *Manis* is widely different from that of the armadillos, and parallels the ground-sloths in some significant features of construction. The astragalar trochlea is somewhat oblique, not so short anteroposteriorly, and the head has developed a concave facet for the navicular, just as in the *Gravigrada*. The fourth digit is much enlarged at the expense of the others; and the distal ends of the metatarsals, like the metacarpals, have developed strong median keels, much resembling the Miocene ground-sloth type.

Measurements

	No. 15086	No. 15137	No. 15088	No. 16831
Skull, length of portion preserved	65.5			
“ width at interorbital region	18.5			
“ “ “ mastoid region	34.8			
“ height, condyles to occiput	23.2			
Cervical vertebræ, length of 7 in series	57.			
Humerus, length				
Radius, length				44.
Ulna, length				
Metacarpal III, length	15.			16.
Femur, length		80.	85.	
Tibia, length		67.5		
Metatarsal, length	19.5			
Pelvis, length		94.3	106.	
Sacrum, length		55.5		
Astragalus, length		13.		
“ width of trochlea		8.3	8.1	
Calcaneum, length				23.

Palæanodon parvulus, new species

Fig. 57

Type.—Amer. Mus. No. 15859, fragments of skeleton including limb and foot bones from Clark Fork beds of Wyoming.

Specific distinctions.—Size one-fourth less than *P. ignavus*, and considerably more slender throughout.

The portions of the skeleton preserved include the entire tibia, the radius

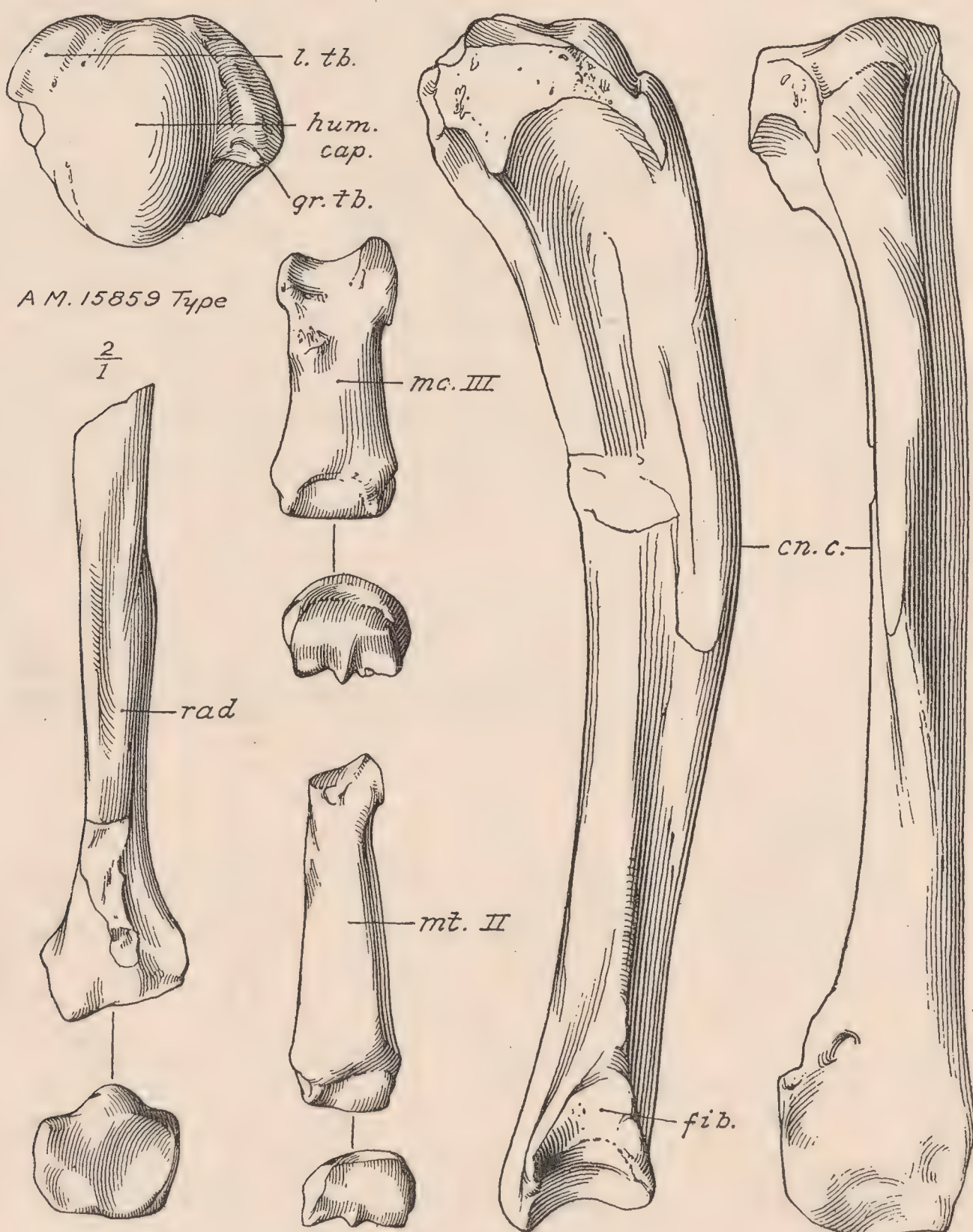


Fig. 57. *Palæanodon parvulus*. Type specimen, No. 15859. Clark Fork horizon, uppermost Paleocene from Clark Fork basin of Wyoming. Twice natural size.

lacking the proximal end, parts of both humeri, mc. III entire, one metatarsal and both ends of another, parts of scapula and caudal vertebræ. The chief interest of the specimen is that it indicates the occurrence of a

smaller and probably more primitive species of this group in the top of the Paleocene. It is too fragmentary to show any important primitive characters, such as might be expected in a species from an older horizon than that of *P. ignavus*, except the small size and slender proportions above indicated.

Geological Range of the Metacheiromyidæ	PALEOCENE			EOCENE					
	Puerco	Torrejon	Clark's Fork	LOWER			MIDDLE		UPPER
				Gray Bull	Lysite	Lost Cabin	L'r Bridger	Up'r Bridger	L'r Uinta Up'r Uinta
<i>Metacheiromys</i> sp. indesc.									
“ <i>dasypus</i>							×		
“ <i>marshi</i>							×		
“ <i>tatusia</i>							×		
? <i>Palæanodon</i> sp. indet.						×			
“ <i>ignavus</i>				×	?				
“ <i>parvulus</i>			×						

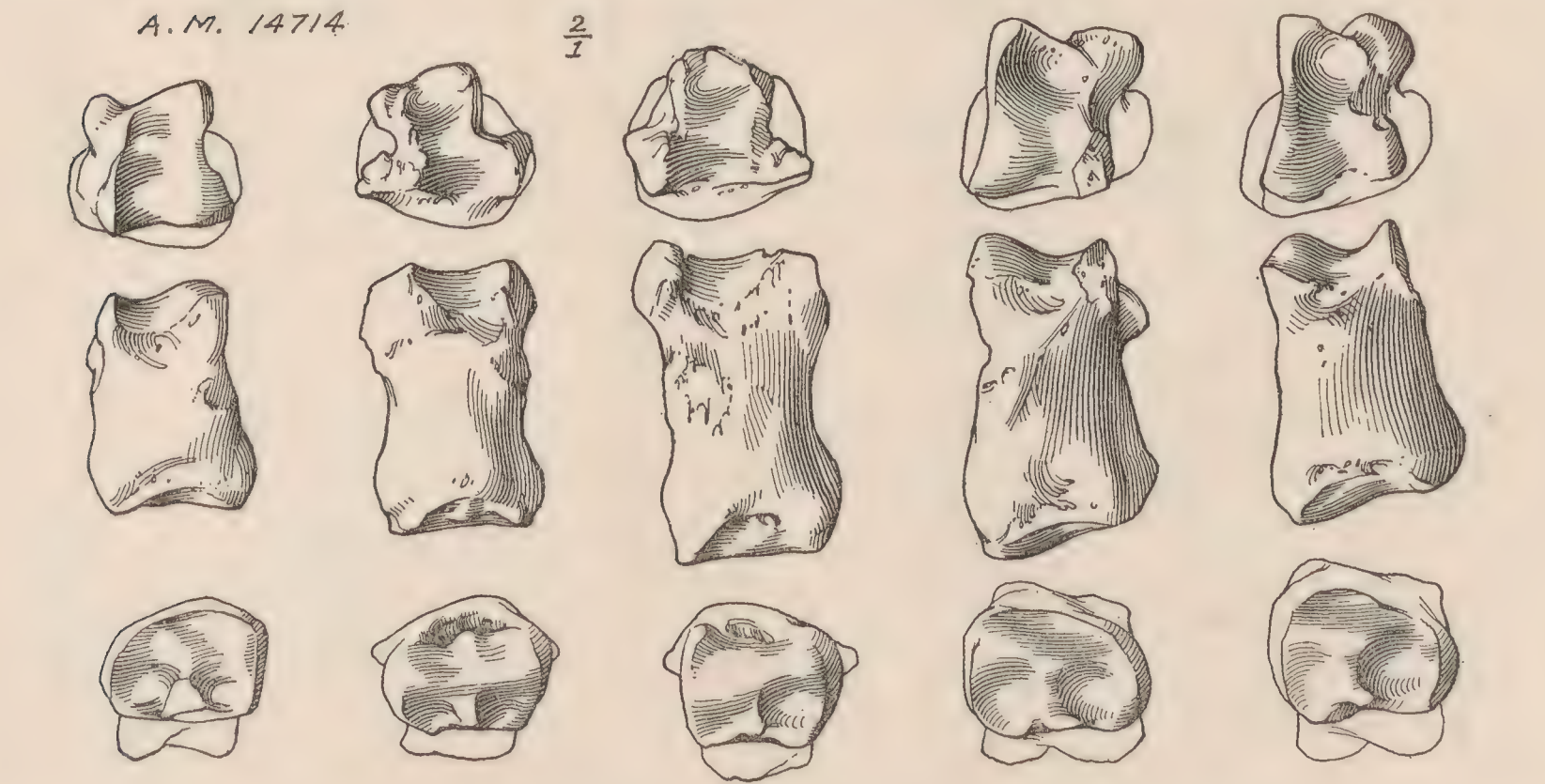


Fig. 58. Palæanodont metacarpals from the Lost Cabin horizon in Wind River basin. No. 14714. Twice natural size.

The principal specimens referred to *P. ignavus* are from the Gray Bull horizon, but there are two specimens from the upper Gray Bull or Lysite, their exact level not being known. In the Lost Cabin three associated lots

of foot bones, Nos. 14732, 14733, and 14734, (Figs. 58-60) and a number of isolated limb and foot bones are recognizable as *Metacheiromyidæ*, and intermediate between *Palæanodon* and *Metacheiromys* in specialization. They represent two or more species, one about as large as *Palæanodon ignavus*, the other about one-fourth smaller. In the smaller species the distal end of the radius has the scaphoid and lunar facets indistinguishable, but the form of the combined facet is subquadrate as in *Palæanodon*, instead of oval as in *Metacheiromys*. The mc. III is shorter than in *P. ignavus*, its proximal facet somewhat more saddle-shaped, but not so deeply warped as in *M. dasypus*; its distal facet is more nearly like that of *P. ignavus*, retaining more of the primitive hinge joint than does *dasypus*. The first and second phalanges of digit III of the manus are of nearly equal length; in *Metacheiromys* the first is shorter. The second metacarpal exhibits a similar intermediate stage of evolution. The astragalus of a larger species has a wider trochlea, shorter anteroposteriorly, and the head has less dorso-

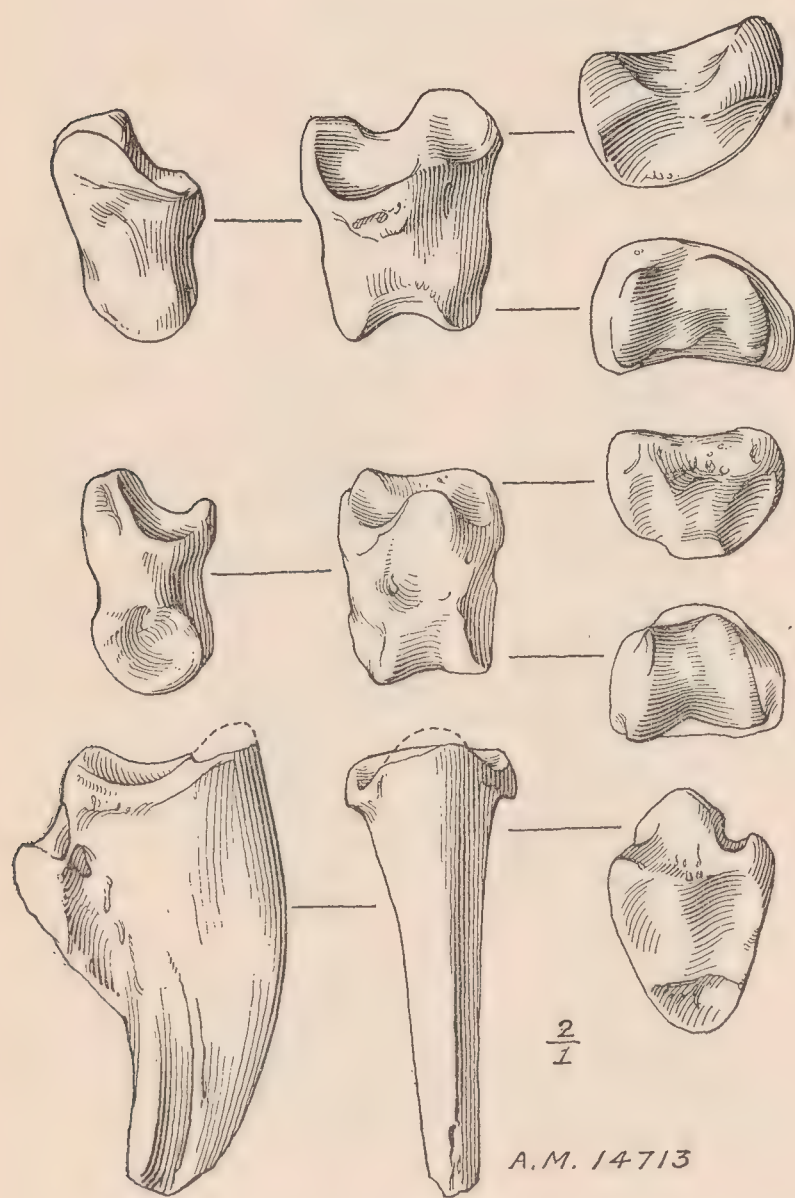


Fig. 59.

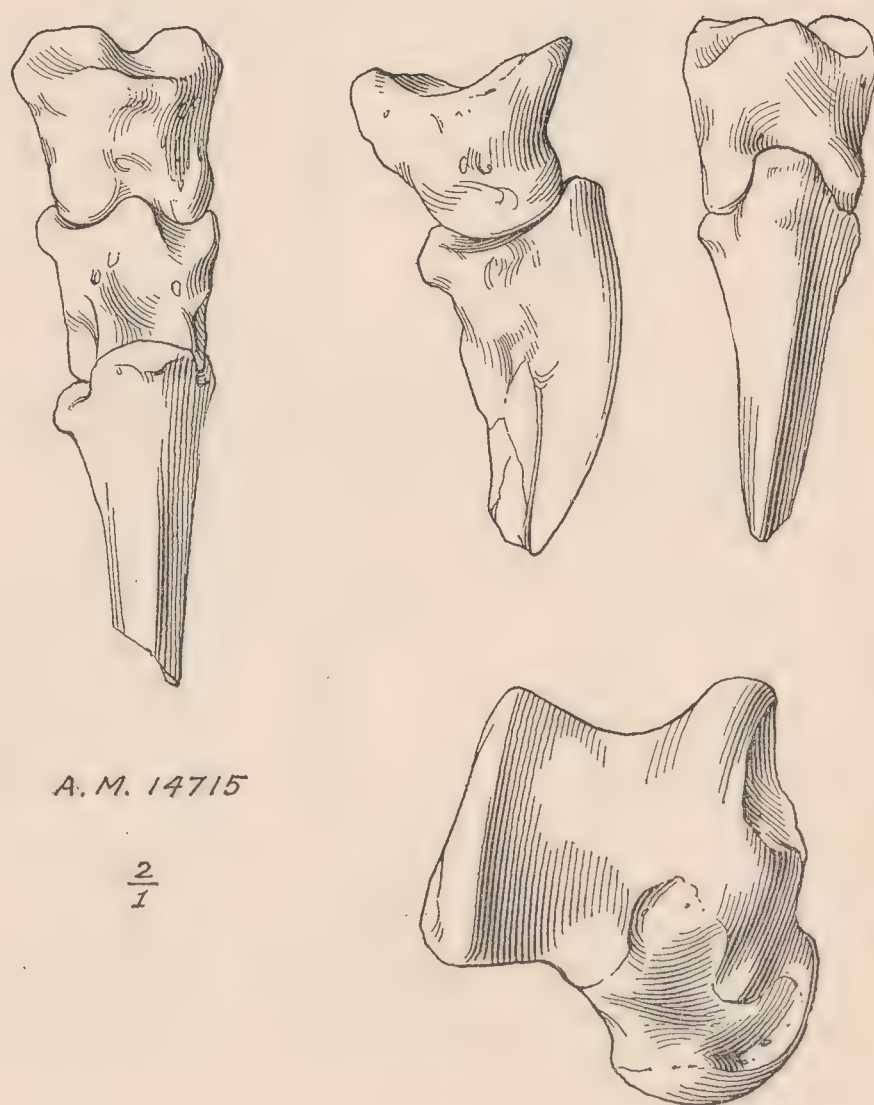


Fig. 60.

Fig. 59. *Palæanodont* phalanges of manus, No. 14713, (associated) from Lost Cabin beds, Wind River basin. Twice natural size.

Fig. 60. *Palæanodont* phalanges of manus, and right astragalus, No. 14715, from Lost Cabin beds, Wind River basin. Twice natural size.

plantar depth. In the absence of skull parts it seems inadvisable to give specific names to any of this material. It serves to show transitional characters to *Metacheiromys* from *Palæanodon*, and thus confirms the derivation of the one from the other.

Affinities of *Palæanodon*

Any consideration of the relationships of this very interesting Lower Eocene genus turns primarily upon the position of *Metacheiromys*, its successor in the Middle Eocene (Bridger formation). Unfortunately, *Metacheiromys* has never been figured or adequately described. The brief diagnosis published by Osborn and Granger in 1904¹ is sufficient indeed, if carefully read and the significance of the stated characters weighed and fairly evaluated, to show that it was a relative of the armadillos. But the diagnosis, unsupported by figures and lengthy detailed descriptions, has failed to carry conviction, and has indeed been apparently disregarded by critics save in the features in which the genus is stated to differ from the armadillos. The two species described in 1904 were based upon admirably preserved specimens, the skull, jaws, and anterior half of the skeleton of a larger species (*M. dasypus*) and the skeleton of a smaller one (*M. tatusia*), less perfectly preserved but sufficiently complete to mount without an undue amount of restoration. There are, in addition, a number of minor specimens from the Bridger formation, which add nothing of importance to its osteology.

There is no question that *Palæanodon* is a near relative of *Metacheiromys*, differing only in various minor characters, some of which have been cited in the foregoing description. Its more general affinities can best be considered after summarizing the principal osteological characters of skull and skeleton.

It appears probable that certain fragmentary specimens from the Oligocene and Miocene of France and Germany, which have been referred to the Edentata by Filhol, Schlosser and Ameghino, may have an important bearing upon the problems here involved. Filhol in 1893² described and figured a number of isolated bones from the Phosphorites which he referred to the Edentata under the names of *Necrodasypus*, *Leptomanis* and *Palæorycteropus*. Schlosser in 1904³ referred to the same order a number of limb and foot bones, some of them associated parts of a single individual, which had

¹ Osborn, H. F. and Granger, W., 1904, Bull. Amer. Mus. Nat. Hist., XX, Art. 12, pp. 163-165.

² Filhol, H., 1893, Ann. Sci. Nat. Zoöl. et Paléont., (7) XVI, Nos. 1-3, pp. 134-139.

³ Schlosser, M., 1904. Notizen über einige Säugethierfaunen aus dem Miocän von Württemberg und Bayern. Neues Jahrb. Beil., XIX, p. 499, Pl. xxvi.

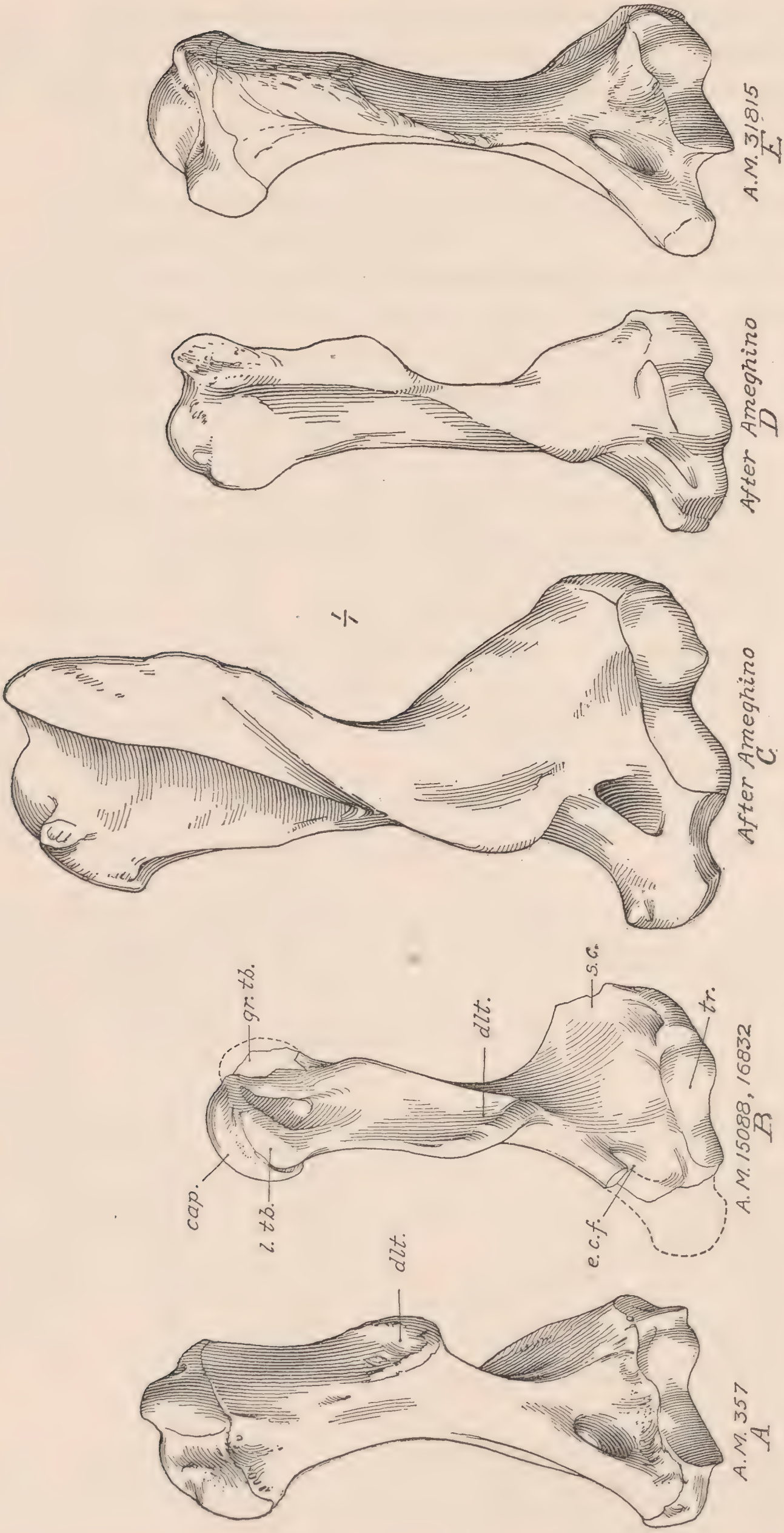


Fig. 61. Comparative anterior views of humeri, natural size, in A, *Dasypus*, B, *Palæanodon*, C, '*Galliatatus*,' D, *Necromanis*, E, *Manis*. The head of the humerus in *Palæanodon* is taken from No. 16832, the remainder from No. 15088. The *Dasypus* and *Manis* humeri are from skeletons in the American Museum; the two European fossils are copied from Ameghino's brochure.

been described some years before by Quenstedt¹ under the name of *Lutra franconica*. Ameghino in 1905² discussed the affinities of these remains, along with some additional fragmentary and non-associated bones from the Miocene of Mont Ceindre near Lyons, France. Some of them he regarded as true armadillos (*Necrodasypus*, *Galliætatus*), others as related to *Manis* (*Leptomanis*, *Teutomanis*) and to *Orycteropus* (*Palæorycteropus*). In a later paper,³ he strongly contested Schlosser's criticism⁴ that the remains referred to *Galliætatus* and *Teutomanis* belonged in large part to the same individual skeleton.

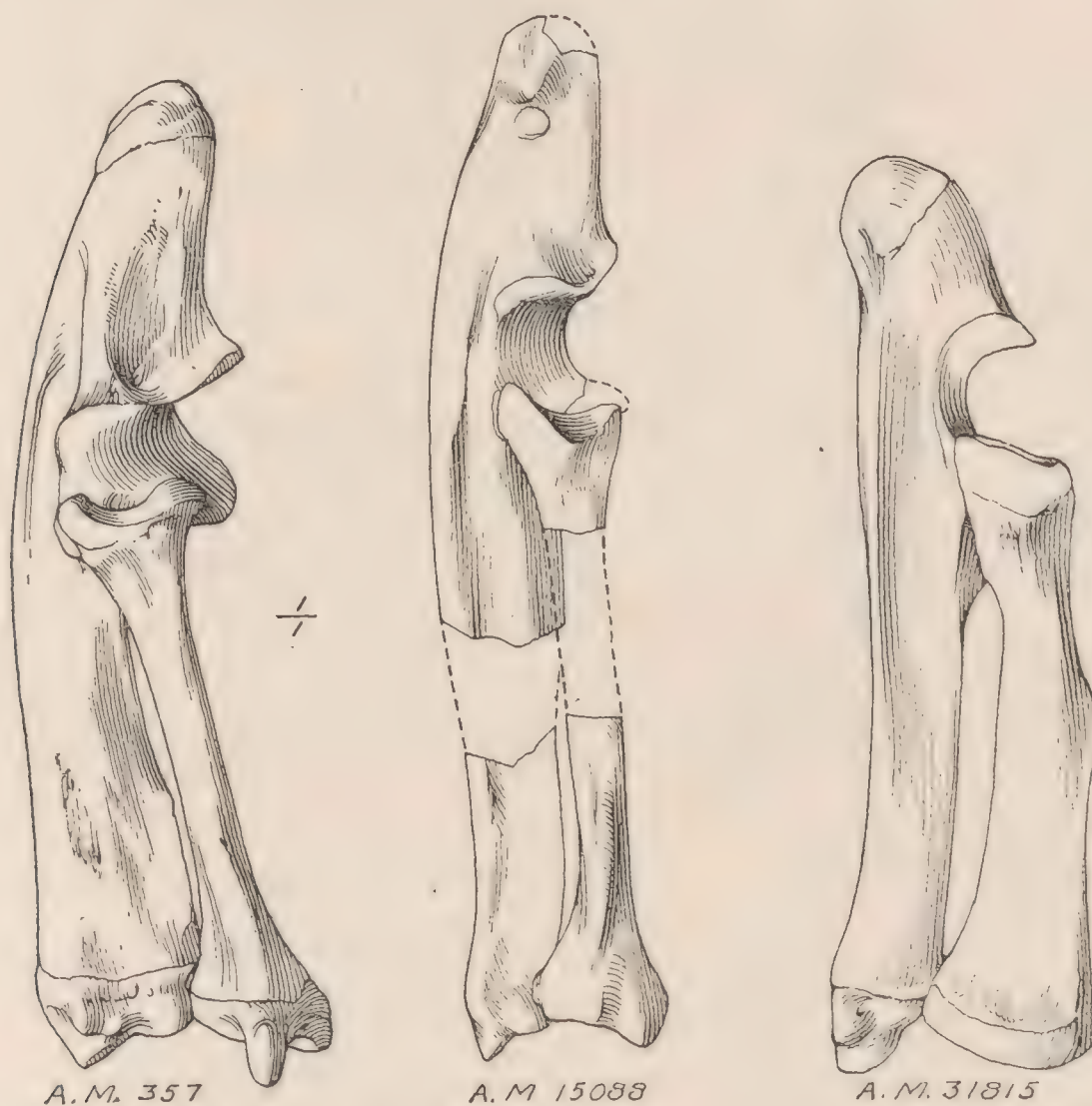


Fig. 62. Radius and ulna in *Dasypus*, *Palæanodon* and *Manis*, anterior views, natural size. From American Museum specimens.

While Ameghino refers the foot bones of "*Lutra franconica*" to the armadillos under the name of *Galliætatus schlosseri*, he regards the limb bones as pertaining to the Pholidota and proposes for them the name of *Teutomanis*. Schlosser, however, (*loc. cit.*) states positively that the foot bones and limb bones pertain to the same individual skeleton, and that the foot bones are metacarpals, and not, as Ameghino holds them to be, metatarsals.

Winge in his recent volume upon the fossil edentates of Lagoa Santa, Brazil, in reviewing the affinities of the various extinct genera, refers briefly

¹ Quenstedt, Fr. Aug., *Handbuch der Petrefaktenkunde*.

² Ameghino, F., 1905. *Les Edentés Fossiles de France et d'Allemagne*. An. Mus. Nac. Buenos Aires, XIII, p. 176.

³ Ameghino, F., 1908, An. Mus. Nac. Buenos Aires, XVII, pp. 104-106.

⁴ Schlosser, M., 1907, *Neues Jahrb.*, I, pp. 462-466.

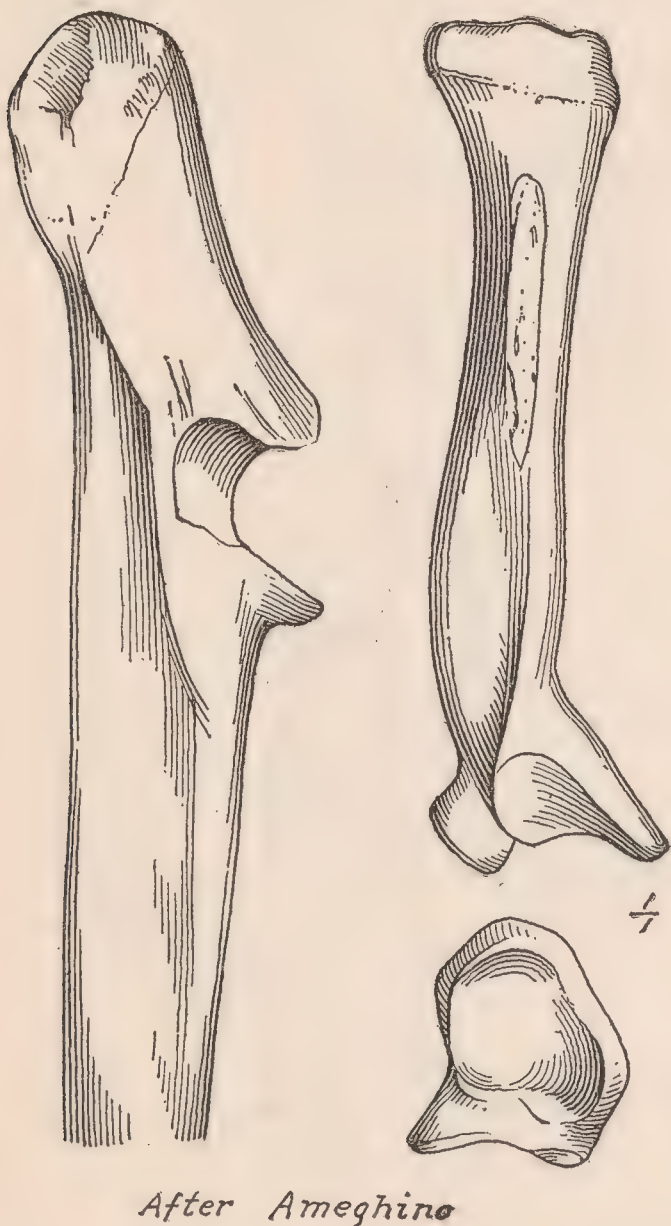
to these European Tertiary remains,¹ and while admitting the armadilloid characters of the foot bones of "*Gallixetatus*," concludes that the characters of the limb bones show that it was nevertheless related to *Manis* and not to the armadillos.

Although regarding the Xenarthra as exclusively American, Winge still ranks both *Manis* and *Orycteropus* with them in the order Edentata, as does Schlosser in his revision of Zittel's 'Grundzüge der Palaöntologie,' 1911.

Most of the recent authorities, however, place them in distinct orders, Pholidota and Tubulidentata, and question or deny any especial affinities between these and the Xenarthra.²

Oldfield Thomas in 1887 advocated raising the New World edentates to the rank of a sub-class Paratheria, coordinate with the remaining Placentalia and the Metatheria, and this arrangement is adopted by Scott (1904, *loc. cit.*, p. 3). Thomas' stated reasons for this classification are confined to certain rather speculative theories concerning the evolution of the milk and permanent dentition in mammals³; Scott presumably accepts the classification upon quite other grounds, as he adopts⁴ the generally accepted theory regarding the origin of the milk dentition.

A careful consideration of the characters and affinities of *Palæanodon* and *Metacheiromys*, in comparison with the armadillos and other Xenarthra, with



After Ameghino

Fig. 63. Ulna of '*Gallixetatus*' and radius of '*Teutomanis*,' after Ameghino. Natural size. The views do not correspond with those in the preceding figure.

¹ Winge, Herluf, 1915. Jordfundne og nulevende Gumlere fra Lagoa Santa, Brasilien. E. Museo Lundii, III, Part 2, p. 306.

² See Flower, W. H., 1882, Proc. Zool. Soc. London, pp. 358-367.

Klinckowström, Axel, 1895. Zur Anatomie der Edentata. Jena, 1895.

Weber, M., 1904, Die Säugethiere, pp. 412 and ff. Jena, 1904.

Smith, Elliott, 1899. The brain in the Edentata. Trans. Linn. Soc. London (2).

Windle, B. G., and Parsons, F. G., 1899. Myology of the Edentata, Proc. Zool. Soc. London, p. 314 and ff.

Mitchell, Chalmers, 1905. Intestinal tract of mammals. Trans. Zool. Soc. London. See pp. 453-458 and 529-530.

Gregory, W. K., 1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., XXVII, pp. 332-341.

³ The arrangement was based upon the view that the diphyodontism of placental mammals was secondarily acquired, a view which Thomas himself withdrew a few years later (Ann. and Mag. Nat. Hist., 1892, p. 308) in consequence of later investigations by Kükenthal and others.

⁴ Scott, W. B., 1913. *Loc. cit.*, p. 94.

Manis and *Orycteropus* and their supposed relatives in the Tertiary of Europe, and with the primitive placentals of the early Tertiary (Eocene and Paleocene, chiefly known from North America), making in this comparison a due allowance for the relative geological age of the various types under consideration, adds a great deal to the evidence for solving the much disputed problems of the origin, relationship and taxonomy of the “eden-tate” orders, and clears up several obscure and difficult points.

Geological and Geographical Distribution of Palæanodonta,
Xenarthra and Pholidota

	EUROPE, ETC.	NORTH AMERICA	SOUTH AMERICA
Recent	<i>Manis</i> (all Oriental and Ethiopian)	<i>Tatusia</i> (Texas, Mexico)	<i>Bradypus</i> <i>Dasypus</i> <i>Tatusia</i> <i>Cholæpus</i> <i>Chlamyphorus</i> , etc. <i>Myrmecophaga</i> , etc.
Pleistocene		<i>Megatherium</i> (Tex., Fla.) <i>Mylodon</i> , <i>Megalonyx</i> <i>Nothrotherium</i> (Cal.) <i>Chlamydotherium</i> (Fla.) <i>Glyptodon</i> , etc. (Fla. & S.)	<i>Megatherium</i> <i>Dasypus</i> <i>Eutatus</i> <i>Mylodon</i> <i>Chlamydotherium</i> <i>Scelidothorium</i> <i>Glyptodon</i> <i>Panochtus</i> <i>Nothrotherium</i> <i>Dædicurus</i> etc.
Pliocene		<i>Megalonyx</i> <i>Glyptotherium</i> Some doubtful frag- ments of ground-sloths	<i>Scelidodon</i> <i>Chlamydotherium</i> <i>Promegatherium</i> <i>Proeuphractus</i> , etc. <i>Palæohoplophorus</i> <i>Neuryurus</i> <i>Lomaphorus</i>
Miocene	<i>Galliætatus</i>	(Absent)	<i>Hapalops</i> <i>Stegotherium</i> <i>Eucholæops</i> <i>Proeutatus</i> , etc. <i>Nematherium</i> <i>Prozædyus</i> etc. <i>Peltephilus</i> <i>Propalæohoplophorus</i> <i>Metopotoxus</i>
Oligocene	<i>Necrodasypus</i> etc.	(Absent)	Ground-sloths doubtful Armadillos imperfectly known
Eocene		 <i>Metacheiromys</i> <i>Palæanodon</i>	Some doubtful fragments of Armadillos
Paleocene		<i>Palæanodon</i>	

Summary of Diagnostic Characters of Palæanodon.—Setting aside generalized or unimportant characters, the following features of the skull and skeleton appear to have principal weight as evidence for the affinity of *Palæanodon*.

1. The cheek teeth appear from their alveoli to have been of armadillo type and considerably reduced in number and size (as in *Tatusia*, *Stegotherium*, etc.), and to have been partly replaced by a horny pad.

2. The front teeth are unknown in this genus. In *Metacheiromys* the canines are large enamelled tusks.

3. The basicranial region is broad and flat; the paroccipital, mastoid, and posttympanic processes are not prominent; and the tympanic region agrees with the general loricate type but also with *Manis*.

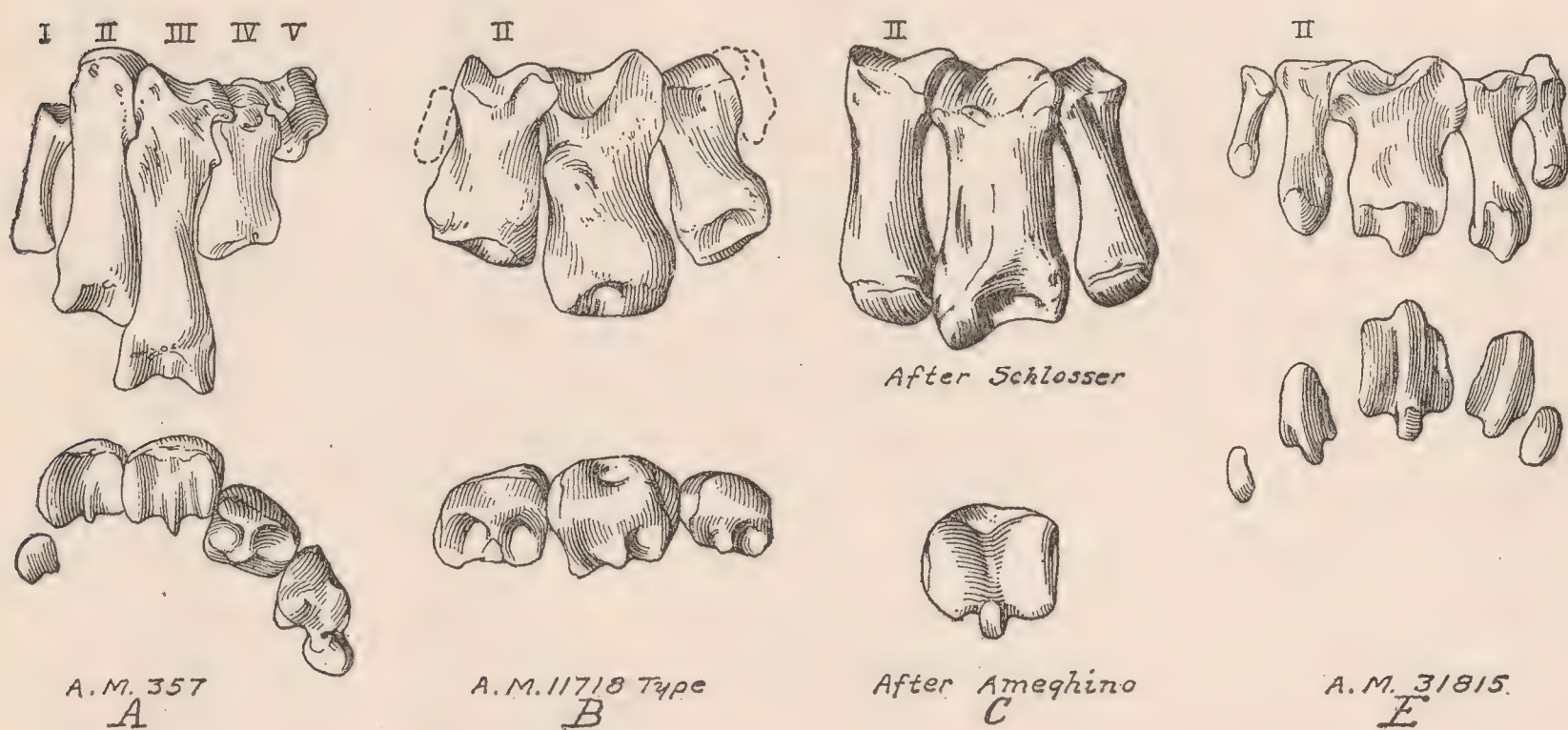


Fig. 64. Comparative views of metacarpals in *Dasypus*, *Metacheiromys*, *Galliaetatus* and *Manis*. The first and the last from the same skeletons as Figs. 61 and 62. The *Metacheiromys* is from the type of *M. dasypus*; the *Galliaetatus* is copied from Schlosser and Ameghino. All natural size.

4. The occiput is broad and low as in *Dasypus*, but the resemblance in this respect is convergent, since the construction in *Dasypus* is decidedly different and the broadening evidently a secondary specialization.

5. The mastoid exposure is extensive both posteriorly and inferiorly, more extensive than in any of the modern armadillos or in *Manis* but of generally similar construction.

6. The foramina for the posterior cranial nerves (condylar and for. lac. post.) are of the primitive insectivore-creodont type, more nearly retained in *Manis* than in the Loricata.

7. The glenoid articulation is like that of the armadillos; the condyle of the jaw is not expanded transversely, the post-glenoid process is vestigial, the socket is more deeply buried than in *Tatusia*, less than in *Dasypus*.

8. The proportions of the lower jaw are armadilloid, somewhat heavier than in *Tatusia*, and the angle projects backward in a sharp process (a primitive character). The front of the jaw is unknown in this genus; presumably it was as in *Metacheiromys*.

9. The cervicals are decidedly short and wide, somewhat as in *Tatusia*, except that C_{2-4} are separate.

10. The dorsals and lumbar are primitive, the zygapophyses with (1) simple flat facets, (2) no accessory facets (i. e. nomarthral), (3) no zygapophysial spines, (4) the spinal nerves making their exit through a notch

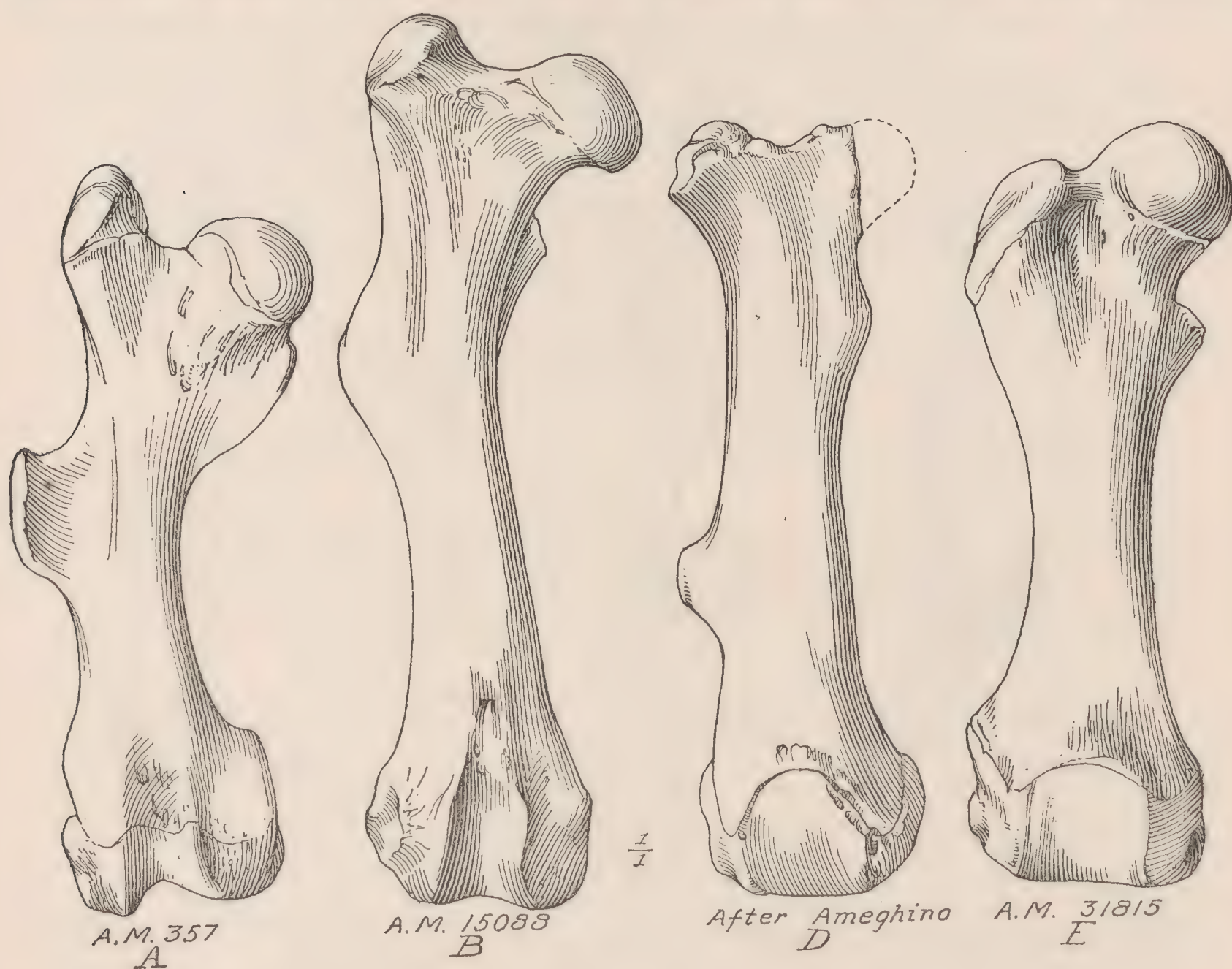


Fig. 65. Comparative views of right femora of *Dasypus*, *Palæanodon*, *Necromanis* and *Manis*. From same specimens as preceding figures; the *Necromanis* after Ameghino. All natural size.

behind the base of the arch, not through enclosed foramina. In all these points they agree with the primitive type, in all except the first with *Manis*, in all except the third with *Metacheiromys*.

11. The caudal vertebræ are likewise primitive but accord much better with the armadillos than with *Manis*; but the tail was very long and heavy.

12. The pelvis is distinctly xenarthral in the long slender anteriorly placed pubis, but the ischium is of primitive type, i. e., long, slender, and not united to the caudal vertebræ.

13. The humerus is distinctly armadilloid in various characteristic details cited in the description, especially the peculiar deltoid crest, prominent supinator crest, and wide shallow trochlea. But the deltoid crest projects forward as in primitive mammals generally, instead of outward as in the armadillos.

14. The ulna is armadilloid in the long, straight, heavy, *Tatusia*-like olecranon and broad flat shaft, but has a reduced and oblique distal facet as in primitive placentals, instead of a wider, transversely set distal facet as in the armadillos.

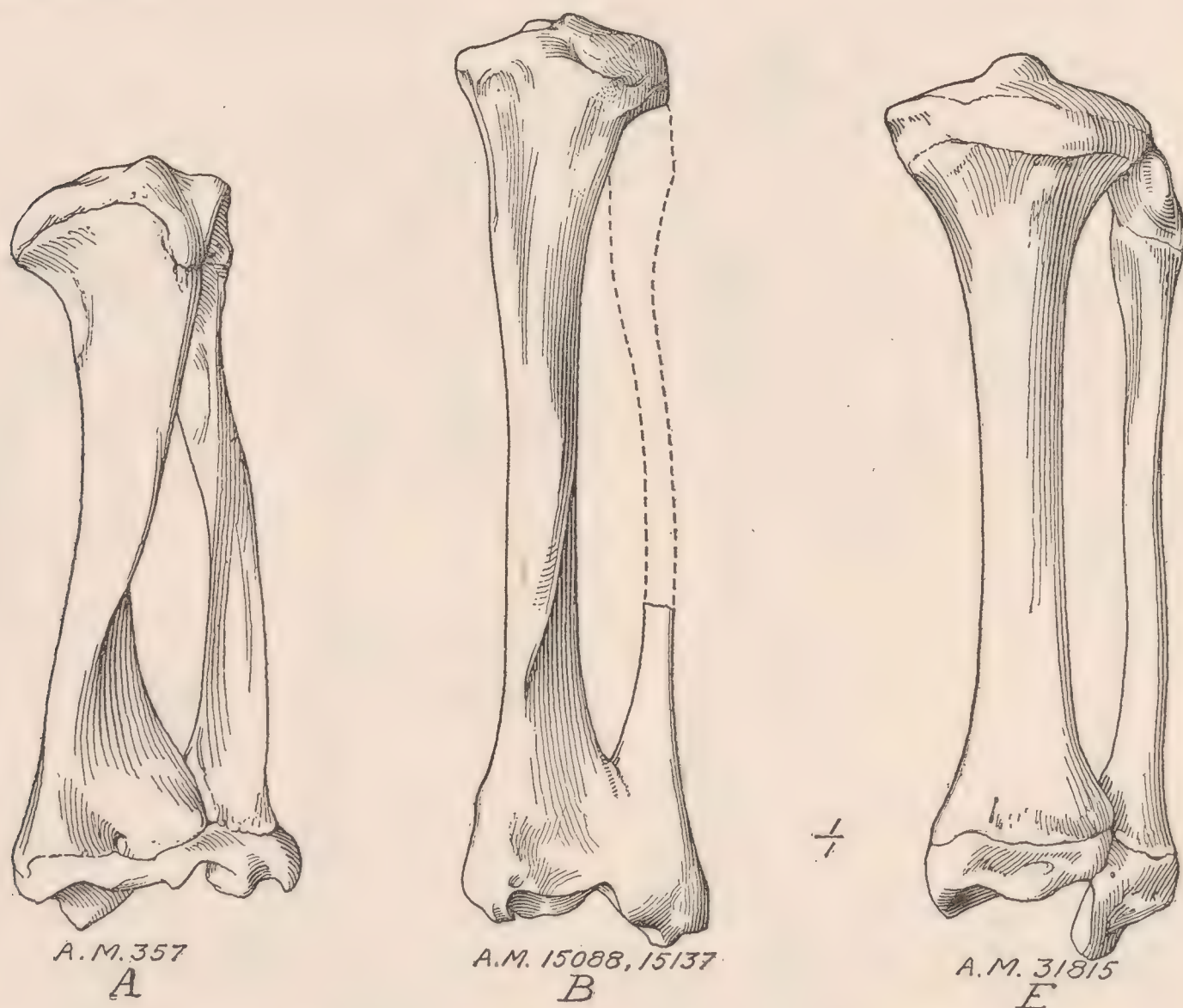


Fig. 66. Comparative views of left tibiæ in *Dasypus*, *Palæanodon* and *Manis*; front view, natural size, same specimens as preceding figures.

15. The radius resembles *Tatusia* in the extremely prominent sharp anterior crest extending from the proximal part of the shaft to the distal end of the bone, the quadrate double distal facet, etc. The crest is directed more anteriorly than in the armadillos (it is higher than in *Dasypus*).

16. The metacarpals are characteristically armadilloid, although more primitive than in *Metacheiromys* or in modern armadillos. This is especially seen in the peculiar distal articulations, the short heavy shafts with prominent dorso-external process, etc. But they retain considerable of the primitive type.

17. The phalanges are armadilloid, about as much specialized in the

manus as *Tatusia*, save that they allow only of a more restricted movement. The unguals, however, are high, narrow and compressed, more of the Miocene ground-sloth type, and not very different from some Eocene creodonts and Insectivora. They are not fissured, save possibly at the very tip.

18. The femur compares well with that of the armadillos, save that the three trochanters are less prominent than in *Tatusia* or *Dasypus*.

19. The tibia is characteristically armadilloid in the forward bowing of the shaft, the high cnemial crest extending along its whole length, the sutural union with the fibula at the lower end, the peculiar form of the astragalar trochlea, etc. It is primitive in lack of proximal union with the upper end of the fibula.

20. The astragalus is like that of the armadillos except that the trochlea is less shortened anteroposteriorly. It is of the primitive insectivore-rodent-edentate type, distinguished by sharp symmetrical crests, no astragalar foramen, wide flattened-oval head, short distinct neck, etc. The

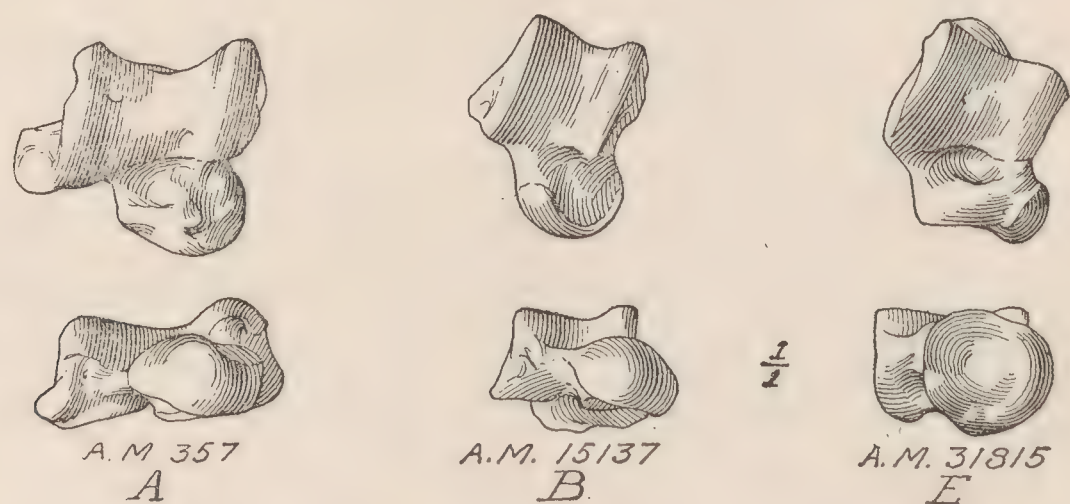


Fig. 67. Dorsal view of right astragalus, natural size, in *Dasypus*, *Palæanodon* and *Manis*. Same specimens as preceding figures.

armadillo-glyptodont astragalus is obviously a specialization from this type; the astragalus in the *Gravigrada* or in *Manis* also appears to be a derivative in a diverse line of specialization. The astragalus of *Orycteropus* appears to be derived not from this type but from the creodont-condylarth type.

21. The metatarsals in *Palæanodon* are very like those of *Metacheiromys*, the internal digit small and slender, the external digit short and stout, the three intermediates being the chief functional digits. This unusual type of lateral digital reduction is characteristic of armadillos. The distal ends of the metatarsals and the phalanges are much like *Dasypus*, etc., but in some respects more primitive.

Relationship to Metacheiromys.—This hardly calls for extended discussion. *Metacheiromys* is more specialized in various particulars but there is no question of its being closely related to, and either directly or approximately descended from *Palæanodon*. The cheek teeth are much more

reduced; the tympanic bulla is completely ossified in the larger species; the limbs and feet more abbreviated, the limb bones, metapodials and phalanges more like those of *Dasypus* or *Tatusia* in various respects; the lumbar zygapophyses develop the characteristic spine of the armadillos,

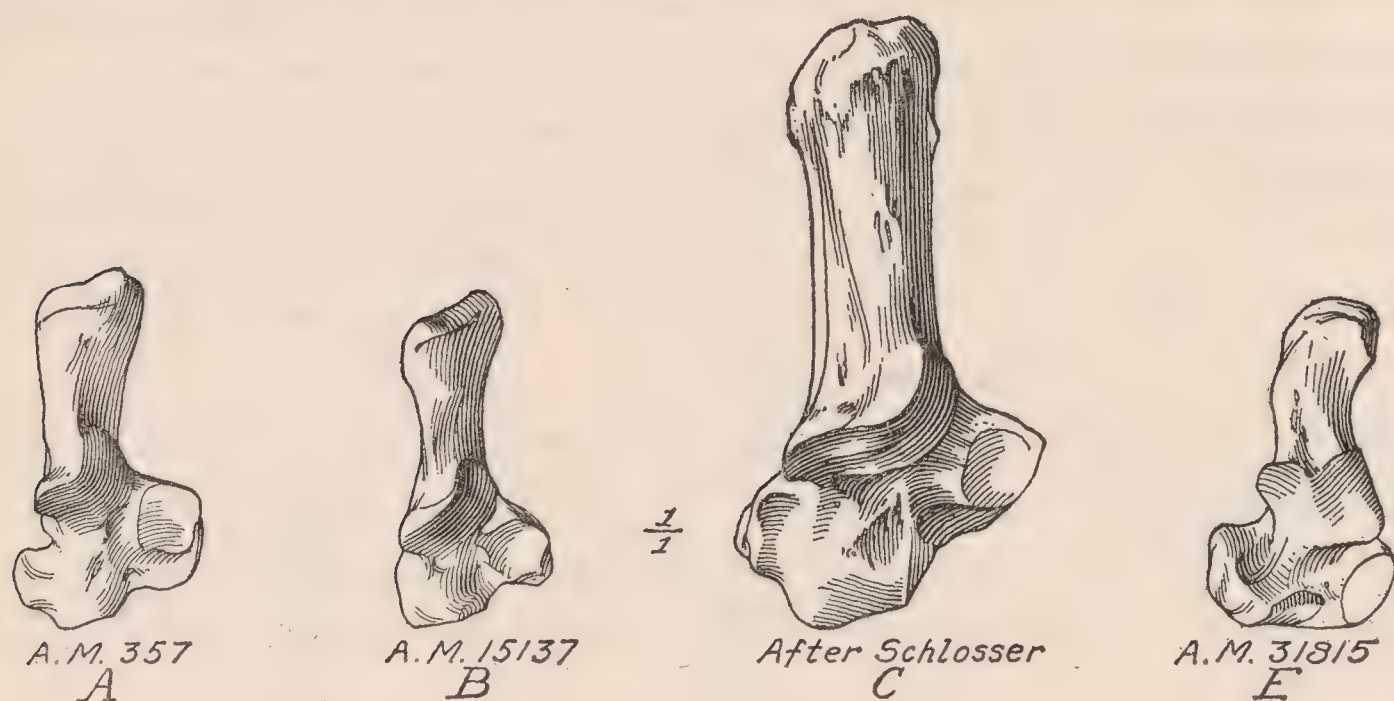


Fig. 68. Dorsal view of right calcaneum, natural size, in *Dasypus*, *Palæanodon*, *Galliætatus* and *Manis*. Same specimens as preceding figures.

although their facets remain flat and the notch for exit of the spinal nerves is not bridged over. The smaller *M. tatusia* retains many of the primitive characters of *Palæanodon* in the basicranial region, vertebræ, and limb bones. It is somewhat smaller than *P. parvulus*, whereas *M. dasypus* is a little larger and much more robust than *P. ignavus*.

The largest *Metacheiromys* is an undescribed species from the Upper Bridger; it is unknown from any later formation.

Relations to the Xenarthra.—From the above list of skeletal characters it appears beyond question that *Palæanodon* is related to the armadillos, although it retains numerous primitive characters that have been lost in varying degree by the late Tertiary and modern genera, and has not developed certain obviously specialized characteristics of all the South American edentates (Xenarthra). It is generally believed, and I think quite rightly, that the armadillos represent most nearly the primitive type from which the sloths and anteaters, as well as the glyptodonts, were derived; and if this be so, the xenarthral articulations of the vertebræ, which appear to be degenerating in the sloths, must have been acquired previous to their splitting off from the common ancestral stock of the Xenarthra, but subsequent to the splitting off of the metacheiromyids from the primitive Edentate stock.

Save for the reduction of the cheek teeth and the supposed character of the canines (the last inferred from the near relationship to *Metacheiromys*),

I see nothing in the skeleton structure against regarding *Palæanodon* as a direct ancestor of the South American Tertiary and modern Loricata, or indeed of all the Xenarthra. It is of course much more primitive; it lacks many of the specializations which are already fully developed in the Santa Cruz genera. But it must be kept in mind that it is a very much older type. It is a contemporary of *Eohippus*. The earliest South American armadillos of which we know the skull or skeleton were contemporaries of *Merychippus* or approximately of that age. Now *Merychippus* is very characteristically equid in numerous features that have not yet appeared or are only vaguely foreshadowed in *Eohippus*, and we must expect to see corresponding differences of degree in phyletic specialization when we compare Lower Eocene with late Miocene representatives in any other phylum. I see no reason to believe that the Lower Eocene and Paleocene ancestors of the Xenarthra were any more specialized than is *Palæanodon* and I believe that they were quite closely related to it. But we know next to nothing of their intervening stages up to the Santa Cruz; for the plates and fragments of isolated bones which Ameghino has described from the Deseado and Casamayor formations and made types of various new genera are too uncertain either of provenience or of association to throw any real light upon the pre-Miocene South American history of the Xenarthra.

For geographic and faunal reasons I do not think that *Palæanodon* was directly ancestral to the Xenarthra even though there were no structural difficulties in the way. The early Tertiary faunas of South America cannot be directly derived from any Tertiary fauna of North America, for they wholly lack true Carnivora, while in the North American faunas from Puerco onward this order was well represented. They must be derived apparently from some late Cretacic fauna, unknown to us but presumably inhabiting some part of North America, and containing the immediate ancestors of our Paleocene and Lower Eocene Condylarthra, Taligrada, marsupials, edentates, notoungulates and perhaps primates and rodents, but not the creodonts, perissodactyls or artiodactyls, Amblypoda or true Insectivora.

Comparison with Manis.—A preliminary comparison of the skeleton of *Manis* with *Palæanodon* and the armadillos had brought me to the conclusion that the pangolins had little or nothing to do with the true Xenarthra, the many points of resemblance in their structure to one or another of the xenarthral groups being due to convergence. A more careful reconsideration and interpretation of the data, and especially the evidence afforded by the supposed "edentate" remains of the Oligocene and Miocene of France and Germany has materially modified that view.

So far as the skull is concerned, there is nothing to prevent our regarding

Palæanodon as a direct ancestor of *Manis*. The cheek teeth are evidently degenerating in the Metacheiromyidæ; in *Manis* they have disappeared; in the lower jaw of the pangolin there is a little bony process very suggestive in character and position of a vestigial remnant of the lower canine tusk of the Metacheiromyidæ. There is a great deal of resemblance in the basi-cranial region; the loss of occipital crest in *Manis* is evidently secondary.

The presacral vertebræ of *Manis* agree fairly well with those of *Palæanodon* except that the lumbar zygapophyses are strongly convex, presumably a specialization. The caudals, however, appear more primitive, extraordinarily so indeed, retaining a uniformly simple, flattened, spine-like transverse process throughout the whole series, while in *Palæanodon*, as also in the armadillos, the same diversity of type in the transverse processes of anterior, median and distal caudals is seen, as in most other primitive mammals and those in general with long heavy tails. But this peculiarity of *Manis* is perhaps reversionary rather than primitive; indeed it points back quite too far to be regarded as truly primitive, for *Manis* is after all a true placental, descended from primitive placental stock, and this character is reptilian and would indicate, if it really were persistently primitive, an independent line of descent back to early Mesozoic Reptilia.

The pelvis of *Manis* lacks that peculiarly xenarthral type of pubis, already indicated in *Palæanodon*; but perhaps this also is secondary, as the incipient union between ischium and transverse processes of the caudals would seem to be; the one character departs from the xenarthral type, the other parallels it.

The limb bones differ greatly from those of palæanodonts and armadillos, and appear at first to be more simple and primitive. But this apparent simplification (decrease of humeral crests, of femoral trochanters, of cnemial crest of tibia, etc.) may also be secondary, and that it is truly so seems to be quite definitely shown in the fossil Manidæ of the European Tertiary, in which intermediate stages are shown.

The peculiar type of astragalus in *Manis* and the prominent distal keels of the metapodials both resemble very closely the Miocene ground-sloths, and differ widely from palæanodonts and armadillos. But these peculiarities in the ground-sloths are undoubtedly derived from the more primitive armadillo type; it is reasonable to conclude that in *Manis* they are also derived from the primitive armadilloid type seen in *Palæanodon*; and here again the European Tertiary genera afford confirmatory evidence, for in *Galliaetatus* the metacarpals appear to be quite armadilloid, although the limb bones of the same skeleton are far advanced toward the type of *Manis*.

On the whole, I can find no very conclusive evidence against deriving *Manis* as well as the Loricata (and through them the remaining Xenarthra)

from the primitive type represented by *Palæanodon*. Just how direct the ancestors may be in each case is a highly speculative matter. But I think that we are well warranted in concluding that there is, after all, a real affinity between the Pholidota and Xenarthra. They may not necessarily be included in a single order but they do clearly belong in the same natural superorder Edentata.

Orycteropus, however, does not belong in this natural group. So far as I am able to judge, it has no particular relations to the edentate-insectivore group, but is descended rather from the creodont-condylarth group of the primitive placentals. I can find nothing in the skull or skeleton that seems to be characteristically edentate, as distinguished from merely primitive. The teeth are unique in structure and there is no hint of their origin in any other mammalian type as far as I know. Lönnberg's interpretation,¹ according to which they represent the root, not the crown, of the ordinary mammal tooth, is the most plausible theory of their origin that I have seen.

It seems to be generally agreed by comparative anatomists that there is no definite evidence in *Orycteropus* to indicate any real affinity with the Xenarthra, nor with *Manis*. Elliott Smith² believes that the brain indicates affinities rather with the primitive ungulates than with unguiculates; and there is some support for this view in the skeleton, at least in so far as condylarthran affinities are suggested. The astragalus has some resemblance to that of the typotheres and some other notoungulates, which would be in accord with this derivation.

Distributional Notes to Accompanying Table

- 1) Pampean formation; South America and North America generally.
- 2) Samos, Maragha; probably Mediterranean region in general.
- 3) Santa Cruz formation, Patagonia; probably South America generally.
- 4) Solenhofen, Bavaria (fissure filling); probably Europe and Asia generally.

5) Pyrotherium fauna (Deseado) of Patagonia; probably South America in general.

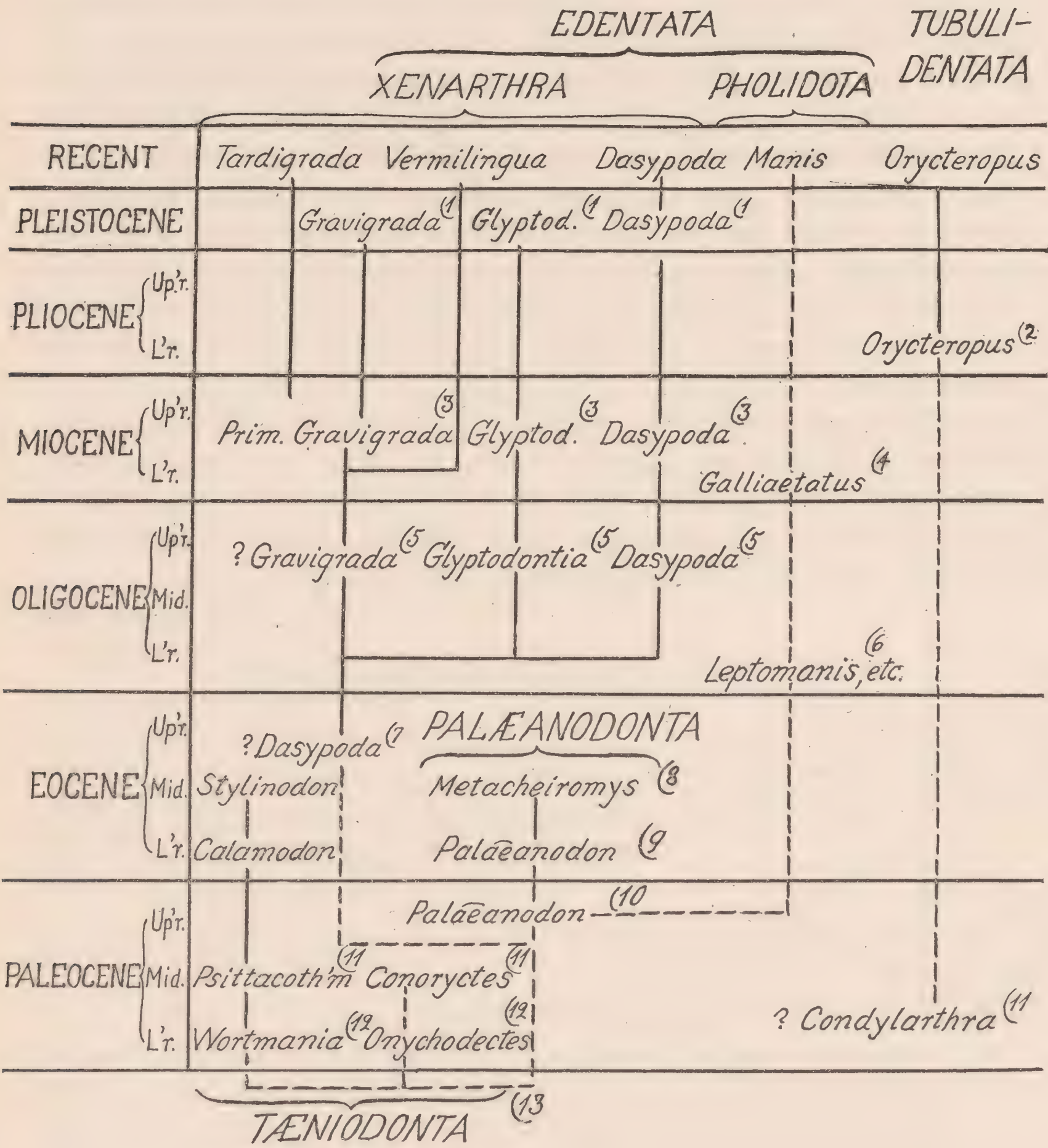
6) Phosphorites, France; probably Europe and Asia.

7) Notostylops fauna (Casamayor) of Patagonia; presumably widely distributed in South America. The armadillos are represented only by isolated plates of the carapace and by parts of bones of questionable refer-

¹ Lönnberg, Einar, 1906. On a new *Orycteropus*, etc. Arkiv. for Zoöl., k. sv. vet. Stockholm, III, No. 3, pp. 1-35.

² Smith, Elliott, 1899, Trans. Linn. Soc. London, (2) Zoöl., VII, p. 387 and ff.

PHYLOGENY OF THE EDENTATA



ence. It is somewhat doubtful whether they really belong in this fauna which has been much confused by Ameghino with the later horizons.

8) Bridger formation of Wyoming. Presumably widely distributed in North America.

9) Wasatch and Wind River, Wyoming and New Mexico. Presumably widely distributed in North America. The scanty Sparnacian fauna of Europe is identical, so far as it goes, with the Wasatch, and there is no valid evidence against extending the distribution of *Palæanodon* to Europe and Asia at this time — nor any proof that it did so extend.

10) Clark Fork, Tiffany, ?Fort Union in part, of Wyoming, Colorado and Montana. Probably widely distributed in North America. The Cernaysian fauna of France is a near equivalent, and in part closely related, but only in part. The most abundant types of the one fauna are absent from the other. This may mean that the Holarctic faunas at this stage were more provincial than in the Lower Eocene when the cosmopolitan Coryphodon fauna replaces them. The great migration between Paleocene and Eocene may have initiated the dispersal and differentiation of the edentate groups.

11) Torrejon of New Mexico, ?Fort Union in part. Probably widespread in North America. The Cernaysian of France is a near equivalent, but apparently somewhat later. There is no sufficient evidence to indicate whether the Phenacodontidæ ever reached Europe, but *Orycteropus* might be derived from this family, although not from *Phenacodus* itself.

12) Puerco of New Mexico. Unknown elsewhere, but presumably widespread in North America, perhaps throughout the northern world. No trace of this fauna has been detected in the Fort Union, which immediately and without any serious stratigraphic or floral break overlies the Lance formation containing a fauna of dinosaurs, multituberculates and didelphoid marsupials. This has suggested that the Puerco fauna is really of equivalent age to the Lance or even older, but represents a different habitat facies. The formation is underlain by beds equivalent to the Belly River, an older horizon of the Upper Cretaceous.

13) Primitive 'Insectivora' related to the *Leptictidæ* and *Pantolestidæ*. Unknown but presumably Holarctic.

Article XVII.—THE TERMITES OF PANAMA AND BRITISH GUIANA

BY NATHAN BANKS

PLATE LI

I.—PANAMA

A number of years ago Mr. P. H. Dudley, who was at work in Panama, became much interested in the white ants of that place and in their ravages to woodwork. He published several papers on their habits and sent specimens to Dr. Hagen, but only a few were identified and these only to genera. In the '50's Motschulsky collected in Panama and in his interesting "Etudes" he named two species of termites. Although he gives only a few words of description, I think they are sufficient to hold the names; if not, the names will be credited to Hagen, who gives a description of one and further notes on the other. Specimens from Motschulsky are in the Hagen collection. While at work on the material from Mr. Dudley I learned that there was material from Panama in The American Museum of Natural History, and Dr. Lutz kindly forwarded it. To my surprise, it was the material collected by Mr. J. Beaumont, from whom Mr. Dudley received much of his material. This Beaumont collection is very much larger than the Dudley collection. Later I received some Panama material from the National Museum, mostly collected by Mr. Busck.

Altogether there are sixteen species known from Panama, the most interesting part being the series of *Cryptotermes* representing three new species of this striking genus. Several of the species are found in various parts of the West Indies, and all of the genera are common in South America. One species, *Kalotermes marginipennis*, extends up into the southern part of the United States.

KALOTERMITINÆ

Kalotermes marginipennis Latreille

A number in the Beaumont collection agree with Texas specimens; also from Taboga Island, June 13 (Busck, U. S. Nat. Mus.).

Neotermes holmgreni, new species

ADULT.—Head rufous; the rest of body rather more yellowish, a soiled dark yellowish. Wings brownish, especially along the costal margin; the three heavy veins near costa are colored like the body. Head plainly longer than broad, polished,

but with a number of scattered, erect hairs, as long as two or three antennal joints. Eyes large, nearly circular, not one-half their diameter from the lower margin of head; ocelli large, elliptic, close to the eyes. Antennæ about as long as the head and pronotum; 17- or 18-jointed; the joints all rather short, the last few longer. Clypeus short, its apical margin rounded. Pronotum plainly a little broader than the head, fully twice as broad as long; the anterior margin strongly concave, the sides rounded, the hind margin slightly convex; the surface with scattered, long, erect hairs. Abdomen polished; each segment with a row of long, erect hairs on its hind border, these hairs more numerous toward the tip of abdomen. Femora moderately slender, but the hind femora stouter than in *N. castaneus*; femora with long hairs, as on body. Tibiæ with only very short and more numerous hairs. Length of body, 6.5 to 7 mm.; with wings, 14 to 14.5 mm.

From Taboga Island, Panama, June 13 (Busck).

Type in Mus. Comp. Zool.; paratypes in U. S. Nat. Mus.

CRYPTOTERMES

Three very distinct species are in the collection, two of them represented by adults.

WINGED

1. Wings with veins at tip without oblique branches, membrane coarsely punctate; body brown; small.....*brevicollis*.
Wings with veins at tip with some oblique branches; membrane very minutely punctate; color pale yellowish.....*dudleyi*.

SOLDIERS

1. Pronotum fully three times as broad as long; mandibles hardly visible from above.....*brevicollis*
Pronotum hardly more than twice as broad as long.....2.
2. Mandibles hardly visible from above; edge of elevation vertical; pronotum obliquely emarginate in front.....*longicollis*.
Mandibles visible from above; edge of the elevation sloping backward; pronotum deeply, roundedly emarginate.....*dudleyi*.

Cryptotermes dudleyi, new species

SOLDIER.—Front of head and the mandibles black, the rest yellowish; front of pronotum dark; antennæ very pale. Head not so much elevated in front as in *C. cavifrons*, the ridge obliquely sloping backward, not roughened above; from the side, the head is nearly twice as long as high and the black ridge is a little uneven or roughened; the surface with scattered erect hairs. Mandibles longer than in *C. cavifrons*, evenly curved, toothed slightly on inner edge, as in the figure. Pronotum hardly twice as broad as long; deeply, roundedly emarginate in front; the surface with many short hairs. Length, 5 mm.

Panama (Dudley; Beaumont).

Type in Mus. Comp. Zool.; paratypes in Amer. Mus. Nat. Hist.

WINGED.—Head pale reddish yellow; abdomen and thorax yellowish; antennæ

and legs paler. Larger than *C. cavifrons*; the head plainly a little longer. Eyes nearly circular, less than their diameter from the lower margin of the head; ocelli small, close to the eyes; although the eye is actually larger than the eye of *C. cavifrons*, the ocellus is not larger than in that species. Pronotum broader than in *C. cavifrons*, nearly twice as broad as long, the sides evenly convex, the front margin concave. Head and thorax with scattered fine hairs, which are longer than in *C. cavifrons*. The radial sector has several oblique branches near its tip to the margin; the median runs into the radial sector about three-fourths the way to tip; membrane very finely punctate, about as in *C. cavifrons*. Length, 10 mm.

***Cryptotermes brevicollis*, new species**

SOLDIER.—Head black in front; the rest of head and the pronotum red-brown; front legs more or less reddish brown; the rest of body and the legs pale. Head (from above) but little longer than broad; the sides parallel, barely constricted in the middle; the front margin elevated, each side oblique and with a deep median incision; the surface smooth. From the side, the head is about one and a fourth times as long as high; elevated on the front edge and behind. Mandibles short, hardly visible from above. Pronotum fully three times as broad as long, with the front margin slightly concave, the hind margin a little convex, the sides evenly rounded. Length, 4 mm.; length of head, 1.1 mm.

Panama (Beaumont).

Type in Amer. Mus. Nat. Hist.; paratype in Mus. Comp. Zool.

WINGED.—Red-brown; antennæ and legs paler. Head longer than broad, flattened in front. Eyes circular, a little more than half their diameter from lower margin of head; ocelli elongate, above the middle, and touching the eye. Antennæ short (broken), the joints very short and broader toward the tip. Head with few short hairs. Pronotum about twice as broad as long; the front margin slightly concave; the sides nearly parallel; the hind border slightly convex; the surface with some erect hairs. Abdomen with a few hairs above and below. Legs very short and stout. Wings hardly twice the length of the abdomen; the surface densely, coarsely punctate; costal venation of three parallel veins, the veins at tip without oblique branches but one or two transverse connections. Length to tip of wings, 6.5 mm.

***Cryptotermes longicollis*, new species**

SOLDIER.—Head black in front, reddish brown behind; front margin of pronotum brownish, the rest pale. Head (from above) scarcely longer than broad, a trifle broader in front than behind, the sides faintly constricted; the front margin elevated, indented in middle, each side rounded; the anterior part of the surface faintly, transversely wrinkled. From the side, the head is about one and one-fourth times as long as high. Mandibles very short, not visible from above. Pronotum about one and one-fourth times as broad as long; the anterior margin slightly obliquely emarginate; the sides narrowed slightly and rounded into the hind margin. Head, 1 mm. long; entire length, 3.5 mm.

Panama, in wood of sill (Beaumont).

Type in Amer. Mus. Nat. Hist.; paratype in Mus. Comp. Zool.

TERMITINÆ

Cornitermes acignathus Silvestri

Soldiers and adults from Cabina, May 22 (Busck). The adult is very similar to *C. striatus*, with a slender fontanelle.

Armitermes armigera Motschulsky

SOLDIER.—Head: main part about as broad as long, much broader than the species figured by Silvestri from South America; nose nearly as long as the head, pointed, thick at base, its upper surface slightly below the plane of the head. The mandibles very slender and strongly curved, with a prominent tooth, which points a little outward, before the middle. Antennæ fully reach the tip of the beak; the first joint very long, the second very much longer than the third or the fourth. Gula broadest at tip. Pronotum with the anterior elevated part lobe-like and hardly one-half as wide as the widest part of the pronotum, and at the tip very faintly indented in the middle; the broad, posterior part of pronotum almost semicircular. Head with a very few short hairs, some on the margin of the pronotum, more on the abdomen. The head is yellowish, the other parts very pale, the abdomen discolored. Length of head, 2 mm.

Obispo, Panama (Motschulsky).

A type is in the Hagen collection. Winged specimens of this genus from Paraiso (U. S. Nat. Mus.) may be adults of this species, but it is not certain that they are.

Coptotermes marabitanus Hagen

In both Dudley and Beaumont collections; a common species in South America.

Mirotermes hispaniolæ Banks

WINGED.—Hard parts red-brown; venter and legs paler; antennæ pale brown; wings yellow-brown. Head no longer than broad, flattened in front. Eyes moderately prominent, circular, less than one-fourth its diameter from lower margin of head; ocelli nearly circular, close to the eyes; fontanelle small, about on a level with the top of eyes. Clypeus prominent, twice as broad as long, deeply indenting the lower face. Antennæ longer than the head; 15-jointed; joints short, the third shorter than the second, the fourth hardly longer than the third. Pronotum not much narrower than the head, twice as broad as long; hardly concave in front; the hind margin straight; the sides but little rounded, not narrowed behind. Body and legs with dense, fine hair. Wings short, bluntly rounded at the tip; median vein not forked; cubital extending out to the tip of the wing. Length to tip of wings, 8 mm.

Panama (Beaumont). The species was based on soldiers from Hayti.

Leucotermes tenuis Hagen

Panama (Beaumont); Obispo (Hassler Exped.). Occurs in South America and the West Indies.

Eutermes debilis Heer

WINGED.—Head, thorax, and abdomen pale reddish brown to dark brown; antennæ and legs pale yellowish; wings brownish. Head a little longer than broad, the anterior margin concave. Clypeus three times as broad as long. Eyes small, not quite circular, about the diameter of an eye from the lower margin of the head; ocelli nearly circular, about their diameter or a little less from the eyes. Fontanelle indistinct. Antennæ 16-jointed; the second, third, and fourth joints all short. Pronotum nearly as broad as the head; the front margin nearly straight; the sides narrowed and rounded into the hind border. Body densely clothed with fine, short, yellowish hair. Wings brown; the median vein forked near the tip; the cubital vein runs out somewhat before the tip. Length to tip of wings, 10 mm.

The freshly transformed specimens have the ocelli close to the eyes; the pronotum is more rectangular, and the color is pale.

SOLDIER.—Similar to *M. struncki*, but the head smaller, although of about the same proportions or perhaps a little broader in front. The mandibles proportionally longer and more slender than in *M. struncki*, the inner edge faintly, minutely dentate. Antennæ nearly as long as mandibles; 13-jointed; the second joint about equal to the third. Pronotum one and a half times as broad as long; deeply incised in the middle of the front, each part rounded; the sides narrowed and rounded into the hind border. Body with short, fine hairs, longer ones on the abdomen. Gula narrowed in the middle, about twice as wide in front. Hind femora slightly thickened. Head yellowish; mandibles dark red-brown, pale on the base; antennæ and body pale. Length of head, 1.4 mm.; of mandibles, 1 mm.

Panama (Dudley; Beaumont).

Termes theobromæ Desneux is probably this species; the soldier Hagen described on page 203 of his Monog. Termit. from Panama, Bates' *T. corticicola* (referred to by Hagen under *T. albidus*), and the soldier described with *T. exiguus* are also this species.

Amitermes medius, new species

SOLDIER.—Head yellowish; mandibles red-brown beyond the middle; antennæ, legs, and abdomen pale. Head a little longer than broad, and broader behind than in front. Clypeus deeply indented in the middle. Mandibles not as long as the width of the head in front; at about the middle of their length is a very distinct tooth, whose posterior edge is less sloping than the anterior edge; tip of mandibles much curved. Head sparsely clothed with moderately long, erect hair. Antennæ nearly as long as the head; 14-jointed; the first joint very long, the next two or three very short. Gula broad, barely narrowed toward the base. Pronotum diamond-shaped,

the anterior part very strongly elevated, the edge margined with hairs. Abdomen with some rather long hairs and denser short hair; legs slender and hairy. Length of head (excluding mandibles), 1.6 mm.

Panama (Dudley; Beaumont).

Type in Mus. Comp. Zool.; paratypes in Amer. Mus. Nat. Hist. I have also seen specimens from Taboga Island (Jennings, U. S. Nat. Mus.).

WINGED.—Reddish brown; soft parts yellowish; wings yellowish brown. Head broader than long, flattened in front. Eyes large, higher than broad, nearly touching the lower margin of the head; ocelli large, slightly elongate, close to the eyes; fontanelle distinct, circular, a little below the top of the eyes. Clypeus prominent, twice as broad as long, deeply and roundedly indenting the lower face. Antennæ longer than the head; 15-jointed; the second, third and fourth joints all short and subequal. Pronotum about as broad as the head between the eyes, twice as broad in front as long; front straight across; sides rounded and narrowed behind to the short hind border. Body with much fine, short, yellowish hair. Wings long and rather broad; the median vein forked one or more times; the cubitus running out on the hind border much before the tip of the wing. Length to tip of wings, 10.5 to 11 mm.

Amitermes beaumonti, new species

SOLDIER.—Head yellowish; mandibles (except the base) red-brown; antennæ, body, and legs pale. Head broad, rounded, but little longer than broad; its sides convex, broadly rounded behind; with numerous, rather long, erect hairs. Clypeus subtriangular, hairy at tip. Mandibles about as long as the width of the head in front, very much curved, slender; on the apical third is a tooth, which is well marked behind but in front grades off into the edge. Antennæ 13-jointed; about as long as the head, very hairy. Gula fairly broad, with parallel sides. Pronotum very much elevated in the front part, bordered with long bristles; laterally angulate. Abdomen and legs with erect hairs. Length of head, 1.1 mm.; width, .85 mm.

Panama (Beaumont).

Type in Amer. Mus. Nat. Hist.; paratype in Mus. Comp. Zool.

Small, black-winged adults from Trinidad River, Panama (Busck, U. S. Nat. Mus.) may be this species.

NASUTITERMES

ADULTS

1. Ocelli about twice their diameter from the eyes.....*cornigera*.
Ocelli larger, nearer to eyes.....2.
2. Eyes large, projecting, hardly two diameters apart.....*pilifrons*.
Eyes small, not projecting, fully three diameters apart.....*ephratæ*.

SOLDIERS

1. Head with numerous hairs.....*pilifrons*.
Head with six hairs.....2.
2. Head nearly black; nose short and very stout at base.....*cornigera*.
Head reddish or reddish brown; nose longer, much more slender at base.
ephratæ.

Nasutitermes cornigera Motschulsky

ADULT.— Close to *N. morio*, but the ocelli are still farther from the eyes, being about twice the diameter of an ocellus distant. It is also close to *N. costalis*, but the wings, which are black, do not show a white stripe, and the muscular impressions below the fontanelle are in a very broad and low trapeze, hardly out of line with each other. The antennæ have the second and third joints about equally short, as in *N. morio*. The pronotum is about as in *morio*, the sides narrowed behind, but it is perhaps a trifle broader in proportion to the length than in that species. The body is densely clothed with short fine hairs. The queens are hardly as black-headed as *morio*, but the males are as dark. The soldier has a moderately short nose; there are six bristles in front, as in *morio*. The antennæ have the third joint much longer than the second or the fourth, which is hardly equal to the second. It agrees with the description of *Eutermes cayennæ* of Holmgren and is possibly that species.

Motschulsky's types from Obispo are before me. Mr. Dudley and Mr. Beaumont took specimens, including several queens; Mr. Busck took males at Trinidad River, May; and Jennings collected the species at Las Cascades.

Nasutitermes pilifrons Holmgren

ADULT.— Closely related to *N. ripperti*, but the ocelli are plainly a little smaller; also related to *N. montanæ* and *N. guatemalæ*, but the ocelli are much smaller. Head dark red-brown; pronotum pale yellowish, but dark in middle of front part; antennæ, legs, and mouth parts pale; abdomen brownish; wings yellowish, as in *ripperti* and allied forms. Head very broad, not much elevated above the eyes. Eyes very large, and projecting in front much beyond the edge of the head, longer than the space to the anterior margin; ocelli small, close to the eyes; fontanelle triangular. Clypeus short. Antennæ 16-jointed; the third joint as long as the second, the fourth about as long. Pronotum fully twice as broad in front as long; front margin nearly straight; sides sloping backward and rounded into the hind margin, which is hardly one-half as wide as the front margin. All the body and legs with fine, short, appressed hair and longer, erect bristles. Length with wings, 15 to 16 mm.

From Cabima, Panama, May 20 (Busck).

Soldiers in Beaumont collection, Trinidad River.

Nasutitermes ephratae Holmgren

ADULT.— Head and other hard parts reddish or reddish brown; legs yellowish; soft parts pale. Head, from in front, longer than broad. Eyes small, circular, well separated from the lower margin of the head, fully three diameters apart, and much more than one diameter from the top of the head; ocelli rather small, slightly elongate, less than their diameter from the eyes; fontanelle small, subtriangular. Clypeus hardly as short as in *N. morio*. Head with both erect and appressed hair. Antennæ short; the second, third, and fourth joints short, subequal. Pronotum about twice as broad in front as long; the sides much narrower behind.

Panama (Beaumont, Amer. Mus. Nat. Hist). This differs somewhat from Holmgren's description, the eyes being less prominent than his descrip-

tion would indicate. The species was described from British Guiana, and specimens from that country agree with those from Panama. Also Cabima, Panama, May 20 (Busck, U. S. Nat. Mus.).

SOLDIER.—Head reddish or brownish red; front margin of pronotum reddish; the rest of the body pale or yellowish. Head longer than broad, scarcely elevated above the nose; nose slender, as long as half the width of the head or more; four bristles above base of nose, and two toward vertex. Antennæ slender; the third joint plainly longer than the second, the fourth equal to the second. Pronotum not indented in front, margined with short hairs. Abdomen with a few long bristles.

Taken from nests with queens at Panama. This appears to be the *N. klinckstroemi* of Holmgren from Surinam, but he says that the fourth joint of the antennæ is as long as the third.

II.—BRITISH GUIANA

During a trip to British Guiana in 1911, Prof. H. E. Crampton and Dr. F. E. Lutz obtained a fairly large collection of termites. Since two are new species and several have not previously been reported from that part of South America, a list of all the species is given here.

Rhinotermes marginalis Linnæus.—Tukeit, July 21 (soldiers).

Leucotermes tenuis Hagen.—Rockstone, July 9.

Cornitermes acignathus Silvestri.—Tukeit, July 18 (soldiers).

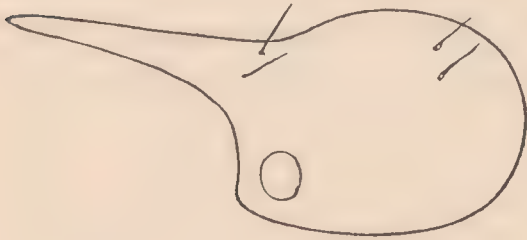
Capritermes cingulatus Burmeister.—Kaietur, August 6 (soldiers).

Nasutitermes ephratae Holmgren.—Tukeit, July 2 and 26 (soldiers and adults). The soldiers agree with the description of *N. klinckstroemi* Holmgren.

Nasutitermes guyanæ Holmgren.—Tukeit, July 17; Kaietur, July 29; Amatuk, August 17; and Tumatumari, July 12 (soldiers). Apparently the most common termite of the region.

Nasutitermes octopilis, new species

SOLDIER.—Head pale yellowish; nose pale reddish brown, darkest at tip; the rest of the body, legs, and antennæ pale yellowish. Head broad, subglobular, very convex as seen from the side; nose slender, acute, nearly as long as the length of the head; four bristles in a curved row over the base of the nose, and two on each side toward the vertex, about their length apart but two or three times as far from opposite pair. Antennæ slender; the third joint plainly a little longer than the second, the fourth hardly equal to the second. Pronotum with the front margin rounded, not emarginate. Abdomen, above, with hairs only along the hind edge of each segment; venter with many hairs. Legs slender, with few hairs. Length, 4.8 mm.; head, 1.8 to 1.9 mm.



From Tukeit, British Guiana, July 17. Differs from *N. aurantiacus* and allied species in the short and more rounded head. Type in Amer. Mus. Nat. Hist.; paratype in Mus. Comp. Zool. "Collected in the forest from a log which was so decayed that little was left but the bark. The interior of the log was filled with soil, detritus, roots, etc. The termite galleries went through into the sandy soil beneath" (Lutz, from field notes).

***Nasutitermes holmgreni*, new species**

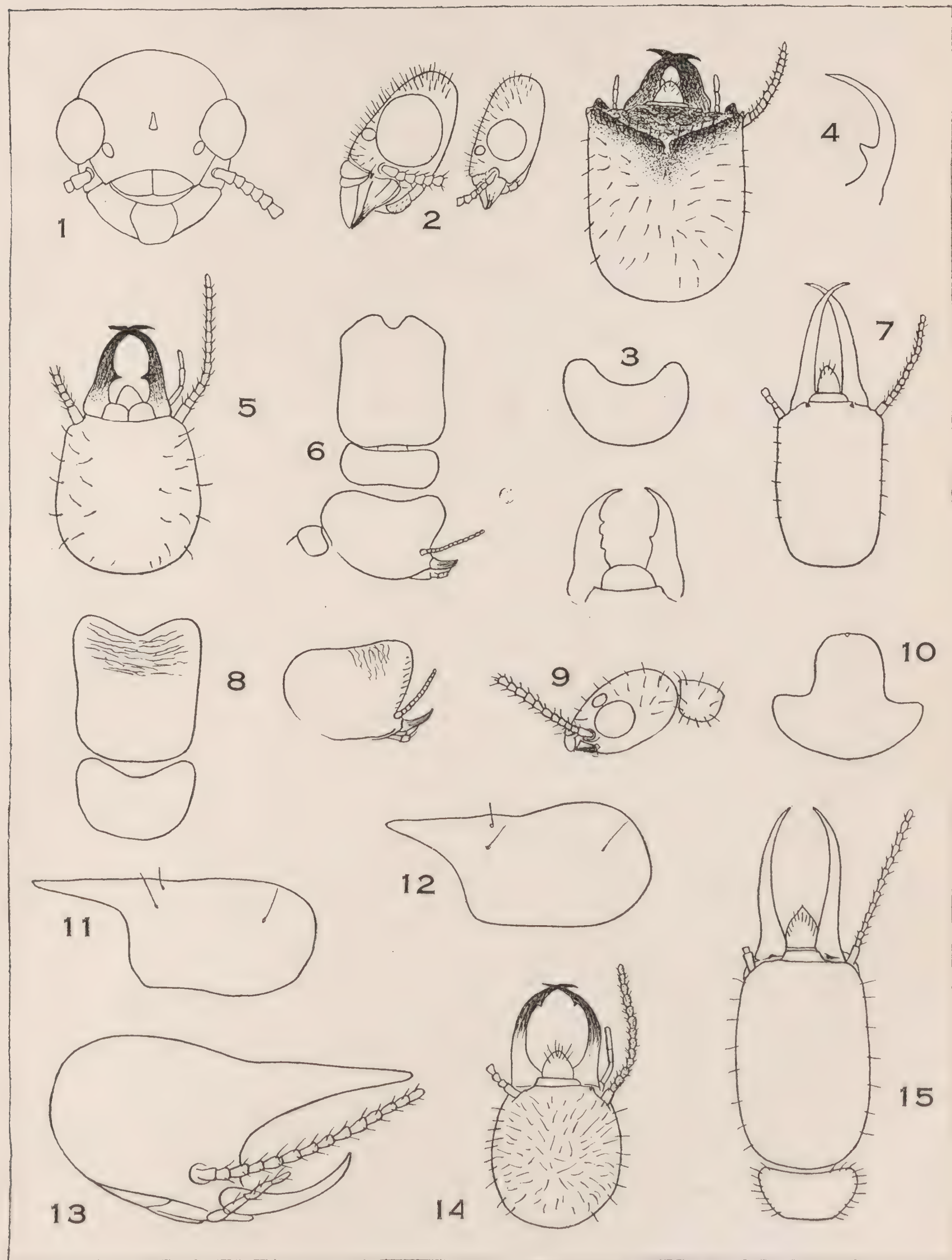
SOLDIER.—Head red-brown, darkest at the base of the nose, paler at the tip of the nose; anterior margin of the pronotum and dorsum of the abdomen brown; venter, legs, and antennæ pale. Head plainly a little longer than broad; nose about as long as two-thirds the width of the head, moderately slender; from the side, no noticeable elevation above the base of the nose. Head, in front, with many, very short, fine, yellowish hairs, and some erect longer bristles, mostly situate above the base of the nose and on each side toward the vertex; no hair on the nose. Antennæ with rather short joints; the third only a little longer than the second, the fourth equal to the second. Front margin of the pronotum rounded, not emarginate. Abdomen, above, with scarcely visible hair, and long bristles at the tips of the segments; venter more hairy. Length, 2.3 to 2.6 mm.; head, 1.05 to 1.1 mm.



From Tukeit, British Guiana, July 19. Distinguished by the small size and pilosity of head. Type in Amer. Mus. Nat. Hist.; paratype in Mus. Comp. Zool. "These termites had a nest on the side of a tree trunk in the forest. The nest was irregular in contour, about three square inches in area, and about half an inch in maximum height" (Lutz, from field notes).

EXPLANATION OF PLATE LI

- Figure 1. *Nasutitermes pilifrons*, head.
 2. *Nasutitermes pilifrons*, at left; *N. ephratae*, at right.
 3. *Cryptotermes dudleyi*, head (above), pronotum and mandibles.
 4. *Armitermes armigera*, mandible.
 5. *Amitermes medius*, head.
 6. *Cryptotermes brevicollis*, head (above and from the side).
 7. *Eutermes debilis*, head.
 8. *Cryptotermes longicollis*, head (above and from the side).
 9. *Neotermes holmgreni*, head (side view).
 10. *Armitermes armigera*, pronotum.
 11. *Nasutitermes ephratae*, head (side view).
 12. *Nasutitermes cornigera*, head (side view).
 13. *Armitermes armigera*, head (side view).
 14. *Amitermes beaumonti*, head.
 15. *Leucotermes tenuis*, head.



Article XVIII.—ON *VOMER DORSALIS*, WITH A BRIEF
[REVIEW OF THE GENUS

BY JOHN TREADWELL NICHOLS

The Genus *Vomer* and its Current Species

Jordan and Evermann in Fishes of North and Middle America,¹ recognize three species of the genus *Vomer* Cuvier and Valenciennes,² a genus of carangin fishes characterized by very deep and strongly compressed form, weak teeth, and very low fins (except in the young of less than 30 mm.). These are *dorsalis*,³ *setipinnis*,⁴ and *gabonensis*,⁵ all three from West Africa and tropical Atlantic America, and *setipinnis* occurring also in temperate Atlantic America and in Pacific America from Cape San Lucas to Peru. They speak of *dorsalis* and *gabonensis* as "doubtful species, not seen by us," and give the following key for the differentiation of the three supposed species.

- a. Soft dorsal with about 25 rays; depth in adult less than half length. . . . *dorsalis*
- aa. Soft dorsal with 21 or 22 rays.
 - b. Depth in adult about half length. *setipinnis*
 - bb. Depth in adult much more than half length. *gabonensis*

Identification of Material from the Mouth of the Congo
as *Vomer dorsalis*

In examining marine fishes collected by The American Museum of Natural History's Congo Expedition of 1909 to 1915 at the mouth of the Congo (Banana) I find a number of small specimens of *Vomer*. These differ from Atlantic American *setapinnis* in having a slightly higher fin count: the dorsal soft rays usually 24, rarely as low as 22 or as high as 25; anal soft rays usually 20, sometimes 19. The thirty specimens examined definitely establish *dorsalis* as a recognizable form. The following table shows the fin counts, and decrease of depth with age.

¹ 1896, Bull. 47, I, U. S. Nat. Mus., pp. 933-935.

² 1833, Hist. Nat. Poiss., IX, p. 189 (*brownii*).

³ *Vomer dorsalis* Gill, 1862, Proc. Ac. Nat. Sci. Philadelphia, p. 436; after Günther.

⁴ *Zeus setapinnis* Mitchill, 1815, Trans. Lit. and Philos. Soc. N. Y., p. 384, N. Y. Jordan and Evermann use the spelling "*setipinnis*."

⁵ *Vomer gabonensis* Guichenot, 1865, Ann. Soc. Linn. Maine et Loire, p. 42, Gaboon.

TABLE I.—*Vomer dorsalis* from the Mouth of the Congo

Length to base of caudal	No. of specimens	Depth		Dorsal soft rays				Anal soft rays	
		Variation	Average	22	23	24	25	19	20
36 to 39 mm.	9	1.3 to 1.4	1.33	—	—	—	—	—	—
40 to 44	13	1.4	1.40		.54	.46		.31	.69
45 to 49	6	1.4 to 1.5	1.45	.16 ² / ₃	.16 ² / ₃	.66 ² / ₃		.67	.33
50 to 59	4	1.5 to 1.6	1.52	.25		.75		.25	.75
60 to 67	7	1.5 to 1.6	1.53	.14	.14	.42	.29	.14	.86
40 to 67	30			.10	.30	.53	.07	.33	.67

No variation of fin count with age in these fully developed fishes is to be expected. That which the figures show may be entirely fortuitous. It is notable, however, that the lot of smallest fishes counted shows a low dorsal mode and little dorsal variation. Probably there are more chances of getting fishes from one lot of eggs in the smaller sizes, before there has been time for the schools to scatter; and a lot with close relationship would be the least variable, and might also show a mode differing from that of the species as a whole.

Consideration and Comparison of Atlantic Material

For purposes of comparison I have tabulated the characters of twelve Atlantic American *Vomer* in the Museum collections of varying sizes.

TABLE II.—Atlantic American *Vomer* (*setapinnis*, and (*) *cubensis*)

Length to base of caudal	Depth	Dorsal soft rays	Anal soft rays	Remarks
37 mm.	1.2	20	—	N. Y. City (dried)
59	1.4	22	18	Porto Rico
72	1.5	22	18	Porto Rico
78	1.6	21	17	Long Island, N. Y.
*112	1.5	22	18	Cienfuegos, Cuba
*119	1.5	22	18	“ “
*122	1.5	22	18	“ “
*122	1.6	22	18	Near Santiago de Cuba
*131	1.6	22	18	Cienfuegos, Cuba
*134	1.6	22	18	“ “
150	1.8	22	18	New York Aquarium
163	1.8	22	?16 (imperfect)	? Cuba

If one runs the eye down the "depth" column, it is noticeable that, after rising to 1.6 for the 78 mm. specimen, the figures (in inverse ratio to the fish's depth) drop to 1.5 for the 112 mm., rise gradually to 1.6 for the 134 mm., then abruptly to 1.8 for the 150 mm. specimen. That is, the 112 and 119 mm. specimens are proportionately deeper than the 78 mm. although half again as large, and the decrease of depth for the 16 mm. between the 134 and 150 mm. specimens is twice what it is for the 22 mm. between the 112 and 134 mm. specimens. The facts of growth for *Vomer* doubtless entail a steady slackening decrease of depth with age, and the great depth of five Cuban specimens between 112 and 134 mm. is due to their being "*gabonensis*" while the others are *setapinnis*. *V. "gabonensis"* is, then, also a recognizable form. It is noteworthy that the small *setapinnis* in the table comparable with the *dorsalis* examined are appreciably deeper than they. The low fin count of the two New York specimens means nothing unless corroborated by more material.

The rather slight differences between the three forms (*setapinnis*, *dorsalis*, and "*gabonensis*"), taken with the individual variation shown to exist in species of *Vomer*, would indicate that these are geographic races rather than full species. Their reputed ranges, however, are almost identical. It is possible that some of the identifications, and consequently the ranges, will have to be revised or that, though the three are found together, each predominates in a certain region.

The use of "*gabonensis*" (based on a single specimen of 70 mm., "*sa hauteur n'étant que deux fois à peine dans la longueur entiere du poisson*") is certainly not justified for the deep-bodied form. We will suppose that Guichenot's specimen was measured from tip of chin to tip of caudal, which would give a maximum length and minimum comparative depth, and compare depths similarly obtained from our material. A Porto Rican *setapinnis* of 76 mm. (59 snout to base caudal) then has depth 1.85, an African *dorsalis* of 70 mm. (55 snout to base caudal) has depth 2.00, *gabonensis* "scarcely twice." Thus *gabonensis* may perfectly well be a specimen of even *dorsalis*, the most slender of the three! Throwing out *gabonensis*, there seems to be no name available for the deep-bodied form (variety A of Günther in part). *Vomer cubensis* is here proposed for it (Type No. 7148 A. M. N. H., length 122 mm.). Further there seem to be no good records for *cubensis* save in tropical Atlantic America.

Young of *setapinnis* alone reach our temperate waters in summer, irregularly but not uncommonly, presumably through the agency of the Gulf Stream, and have been noted as far north as Saco, Maine (Batchelder). Of their occurrence in Rhode Island, Tracy says:

Of various abundance in different years. Adults usually rare. Occasional specimens in August, September and October. Usually much more frequent than *Selene vomer*. . . . In 1906 a remarkably large number of these fishes were present in Rhode Island waters, from the first of August until the last of September. In this season also, adults were numerous. . . . A male specimen taken in West Passage trap, Narragansett Bay, September 11, 1906, gave milt on gentle pressure.¹

According to Lütken *Vomer setapinnis* reaches a length of about two feet.²

Description of the Deep-bodied *Vomer*

I have selected one of the Cienfuegos specimens for detailed description of the deep-bodied form as follows.

Vomer setapinnis cubensis, new subspecies

Argyreiosus setipinnis var. *A.* (in part), GÜNTHER, 1860, Cat. Fishes, II, p. 459. San Domingo to Bahia.

Vomer gatonensis JORDAN AND EVERMANN, 1896, Bull. 47, I, U. S. Nat. Mus., p. 934. NICHOLS, 1912, Bull. Amer. Mus. Nat. Hist., XXXI, p. 186. Not of Guichenot.

Type No. 7148 A. M. N. H. collected in the market, Cienfuegos, Cuba, March 6 or 7, 1912. Length to base of caudal, 122 mm. Head, 2.8 in this length; depth, 1.56. Length of pectoral, 2.6. Eye, 3.4 in head; preorbital, 2.3; maxillary, 2.4, length of peduncle, 3.2; longest dorsal ray, 3.0. Longest anal ray, 1.1 in eye; longest anterior dorsal spine, 4.0; ventral, 2.0; depth of peduncle, 1.7. Dorsal VI–I, 22. Anal II, 18. Scales very small, those on peduncle somewhat larger, the lateral line peduncular scales very weakly keeled. Upper profile with a slight reentrance below eye (so that broad snout is somewhat projecting) almost vertical to nape directly above eye, thence horizontal to origin soft dorsal, thence rounding downward to peduncle. Lower jaw projecting. Lower profile rounding downward and backward with diminishing convexity to front of anal, thence rising obliquely, almost straight, to peduncle. Anterior convexity of lateral line, 1.2 in straight portion to base of caudal. Greatest breadth of body through the anterior portion of the back. Anterior profiles trenchant.

Examination of Pacific Material

The United States National Museum has kindly loaned seventeen specimens of *Vomer* from the Bay of Panama for comparison with our Atlantic material (U. S. N. M. Nos. 29162, 41183, 41190, 41206, 41212, 41213, 41228, 41239, 41388, 43411, 76834, 76835). Their characters have been tabulated (Table III) to compare with those of *dorsalis* (Table I) Atlantic *setapinnis* and *cubensis* (Table II).

¹ Tracy, H. C., 1910, Fishes of Rhode Island. 40th Ann. Rept. Comm. Inland Fisheries R. I., pp. 111–112.

² *Spolia Atlantica*, 1880, p. 605.

TABLE III — *Vomer* from U. S. National Museum, collected in the Bay of Panama

Length to base of caudal	No. of specimens	Depth		Dorsal soft rays				Anal soft rays		
		Variation	Average	21	22	23	24	17	18	19
39 mm.	1	1.3	1.30	—	—	—	—	—	—	—
40 to 44	3	1.3 to 1.4	1.33			.67	.33		.33	.67
64 to 70	3	1.5 to 1.6	1.53		.33½	.33½	.33½		.67	.33
106 to 170	8	1.8 to 2.0	1.90	.12½	.37½	.50		.12½	.62½	.25
215 to 260	2	2.1	2.10		.50	.50			1.00	
40 to 260	16			.06	.31	.50	.13	.06	.63	.31

It will be seen that from the figures these Pacific fish are insignificantly more slender than Atlantic *setapinnis* of the same size, corresponding very closely in depth (for the smaller sizes) with *dorsalis*; and they are notably more slender than *cubensis*. The six specimens of Atlantic *setapinnis* have dorsal rays 22 ($.66\frac{2}{3}$), 21 ($.16\frac{2}{3}$), and 20 ($.16\frac{2}{3}$); that is they average about a ray less than those from Panama, in the dorsal. The four in which the anal has been counted satisfactorily have its rays 18 (.75), and 17 (.25) — again a trifle less, though the mode is the same. Pacific fish represent a geographic variation towards African *dorsalis*,¹ not sufficiently marked to be recognized in nomenclature, and they should stand as *setapinnis*, which they most closely resemble and to which they are most closely allied.

Relationship of *Vomer* to its Specialized Allies and to
More Primitive *Caranx*

Lütken places *Vomer setapinnis* (the one species he recognizes) in the same genus with *Selene vomer*. There is no doubt that the two are closely related. They are probably equally closely related to *Hynn timer*, a somewhat more primitive fish, and the three are specializations of *Caranx*, compressed deep-bodied, with reduced scales and teeth. The following table compares the three with *Caranx*.

Also according to Lütken, *Alectis* is the young of *Hynn timer*, in which case *Alectis* has priority. Doubtless from lack of material, he did not demonstrate this as conclusively as he did the changes of age in *Selene vomer* and *Vomer setapinnis* and the view is not accepted by Jordan and Evermann for the American species. It is incorporated hypothetically in the table, and in the following discussion.

¹ See Nichols, 1916, Am. Naturalist, L, Sept., pp. 565, etc., for discussion of "foreign intermediate" forms.

TABLE IV.—Comparison of *Hynnys*, *Vomer*, and *Selene*

	Soft dorsal and anal		Spinous dorsal		Ventral		Scutes	Body
	in adult	in young	in adult	in young	adult	young		
<i>Hynnys goreensis</i>	moderately falcate	streamers anteriorly (<i>Alectis</i>)	absent	reduced (<i>Alectis</i>)	moderate	large (<i>Alectis</i>)	reduced	deep (especially in young = <i>Alectis</i>) and compressed
<i>Vomer setapinnis</i>	very low	moderately falcate	low	anterior rays high	very small	large	vestigial	very deep (especially in young) and compressed
<i>Selene vomer</i>	falcate produced	moderately falcate	low	anterior rays produced	very small	large produced	absent	very deep (especially in young) and compressed

Some tendencies to specialization in these fishes are (1) towards a deep and compressed body, (2) reduction of peduncular scutes, (3) elongation of ventral fins, (4) production of spinous dorsal, (5) elongation dorsal soft rays. In the reduction of scutes (2) there is simple progression, *Hynniss*, *Vomer*, *Selene*; and, in general, it is most convenient to consider the three increasingly specialized in the order named. Applying this to deepening and compression of body (1), we find *Vomer* and *Selene* about equally more specialized than *Alectis-Hynniss*. In this respect all three become less specialized with age. It is notable that the young are much more abundant than the adults and, taken collectively, they may be considered as the vegetative or somatic portion of each species, in which specialization has been most rapid, adults lagging behind. In elongation of the ventral (3) in the young, *Selene* is most specialized, *Hynniss* and *Vomer* about equally less so. A complication is introduced by the very small ventral of adults of *Vomer* and *Selene*. This reversal of the specialization tendency may be a physiological corollary following exhaustion after early development. As regards the spinous dorsal (4), there is regular progression in the young, here paralleled by that in the adult. It will be noted that in this respect both *Alectis-Hynniss* and the adults of *Vomer* and *Selene* are below the specialization plane of ancestral *Caranx*. This may be explained by supposing that the common ancestor of our three genera was below that plane. The condition in soft dorsal and anal (5) is most complicated. It is highly specialized in *Alectis* (young), normal in *Hynniss* (adult). In *Vomer* and *Selene* young it is normal. This is the one character taken up which would lead one to suppose them less rather than more specialized than *Alectis* (*Hynniss*). The adults of *Vomer* and *Selene* are sharply contrasted here: *Selene* highly specialized (fin falcate, produced), *Vomer* reversely specialized (fins very low). The produced soft-dorsal of adult *Selene* is of very different character from that of *Alectis* (young) and shows no close relationship between the two.

With this review of conditions shown in the table, I will attempt to construct a phylogeny of the three genera. *Hynniss* (adult) is nearest the ancestral form (which I will call *Caranx prohynniss*). *Hynniss* is unquestionably primitive and most readily placed in *Caranx*, some species of which it resembles rather closely. There was a sharp differentiation adaptation after *C. prohynniss*; the *Alectis-Hynniss* fork reversed the general tendency by reduction instead of increase of the spinous dorsal, and lost the tendency to deepening of the preorbital portion of the head found in the other fork. *Vomer* and *Selene* are more closely allied to one another than to *Alectis*. Their general specialization has proceeded as sketched above. Their divergence in the high and low soft dorsal of the adult is a differentiation

adaptation, not an environmental adaptation or general evolutionary tendency. The suppression of spinous dorsal in *Hynn timer* (adult), produced soft dorsal of adult *Selene*, and reduced soft dorsal of adult *Vomer* are all specializations which are differentiation adaptations. The fact that they reverse the custom of the environmental or evolution tendency specializations to be most marked in the young is correlated with this fact.

Summary

To sum up the writer's conclusions from the material examined: *Vomer* and *Selene* are both derivatives of *Caranx* through *Hynn timer*, and all four genera separable. Three valid forms of *Vomer* exist, as differentiated by Jordan and Evermann on variation in depth and fin rays: *dorsalis*, *setapinnis*, and *cubensis* (= *gabonensis* J. and E., not of Guich.). There is great age variation in depth and considerable individual variation in fin rays. The three forms are close and probably overlap in characters, rather than in ranges to the extent supposed by earlier authors; though, as their migrations, aided by ocean currents, are considerable, this is not certain. *Dorsalis* is the West African form; *setapinnis*, American, both Atlantic and Pacific; *cubensis* West Indian (Cuba). The three should stand as subspecies of *setapinnis*. Pacific *V. s. setapinnis* differs slightly but not recognizably from that of the Atlantic. Following is a revised analysis of the three forms.

a. Depth in adult about half length, or less.

b. Dorsal soft rays usually 24 (22-25). Anal usually 20 (19-20).

Vomer setapinnis dorsalis.

bb. Dorsal soft rays usually 22 or 23 (20-24). Anal usually 18 (17-19).

Vomer setapinnis setapinnis.

aa. Depth in adult much more than half length. Dorsal soft rays 22. Anal 18.

Vomer setapinnis cubensis.

Article XIX.—SOME MARINE FISHES FROM NORTHWEST GREENLAND¹

BY JOHN TREADWELL NICHOLS

The Crocker Land Expedition of 1913–1917, sent out under the joint auspices of The American Museum of Natural History, the American Geographical Society, and the University of Illinois, brought back several species of marine teleost fishes from the northwest coast of Greenland. Most of the specimens were collected by Dr. M. C. Tanquary, Zoologist of the expedition.

COTTIDAE

Icelus bicornis (Reinhardt)

There are six small specimens of this sculpin, all from Etah. Two, 25 and 30 mm. in total length to tip of caudal fin, were taken in July or early August, 1914. Four others, 28, 29, 36, and 40 mm. respectively, were

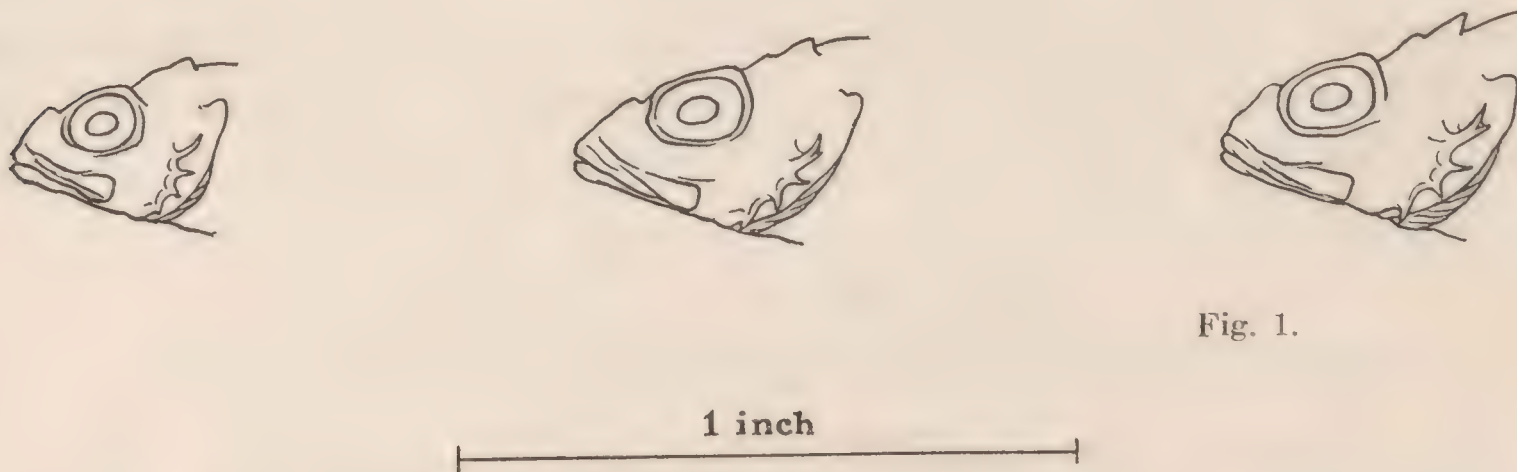


Fig. 1.

Fig. 1. *Icelus bicornis*, to show development of preopercular spine.

taken on Sept. 7 of the same year. The development of the upper preopercular spine with age is interesting. In the four of from 29 to 30 mm., it is simple and curved upward. In the one of 40 mm., it is two-pronged, as is characteristic of the adult, the prongs being of almost equal length. The 36 mm. fish shows an intermediate condition with a distinct lower prong, which is shorter than the original upper one. The three stages are shown in the figure.

¹ Scientific Results of the Crocker Land Expedition.

Myoxocephalus scorpioides (Fabricius)

There is a single specimen, 170 mm. in total length to tip of caudal, which differs from the numerous *groenlandicus* in stouter body, skin without asperities, more numerous small pimples on the top of the head, fewer anal rays, smaller mouth, narrower fold of the gill membranes, and weaker spines.

As it is rare to find adequate series of Greenland fishes in collections, a detailed description of this specimen may be of use to some future student.

Head in length to base of caudal, 3.0; depth, 2.5. Eye, in head, 5.0; interorbital, 5.5; snout, 3.5; maxillary, 2.5; pectoral, 1.0; ventral, 1.7; caudal, 1.8; longest dorsal spine, 2.5; longest dorsal ray, 2.2; longest anal ray, 2.5.

Spines of the head small, those on top of the head very low, the pair above and behind the eye and at the nape each with a small tentacle. Gill membranes narrowly joined to the center of the isthmus, forming a very narrow fold at this point. No slit behind the last gill. Skin smooth, except for the concealed membranous plates (common to the genus) along the lateral line and numerous small pimples which cover the top of the head. Dorsal IX-I, 15. Anal, 11.

Color, in alcohol, above and on the dorsal fins, dull grayish, obscurely mottled with darker. Pectoral and caudal more or less marked with dark and whitish; ventrals whitish, with a few faint gray markings. Anal whitish, marked with dark gray. Chin dusky, underparts otherwise whitish.

Myoxocephalus groenlandicus (Cuvier and Valenciennes)

This seems to be the commonest shore sculpin in the region. There are thirteen adult specimens, which are referable to it, from 200 to 340 mm. in total length to tip of caudal fin. Of these, four have 13 anal rays and nine have 14. The interorbital width varies as follows, quite independently of the size of the fish. Two have it contained in the head 6 times; three, 5.7 times; four, 5.5 times; one, 5.2 times; and three, 5.0 times.

Two of the four with 13 rays in the anal are from Umanak. Another specimen, a male, without definite data, is aberrant, in that it has the warty nodules larger and more regularly placed, interorbital more concave (6.0), dorsal more solidly black, than is usual.

Aside from this one individual, there seems to be comparatively little variation in them except that which is sexual: males have much larger dorsal fins and are brighter, more contrasted, more black and white in color. I have examined the stomach contents of a male and a female of approxi-

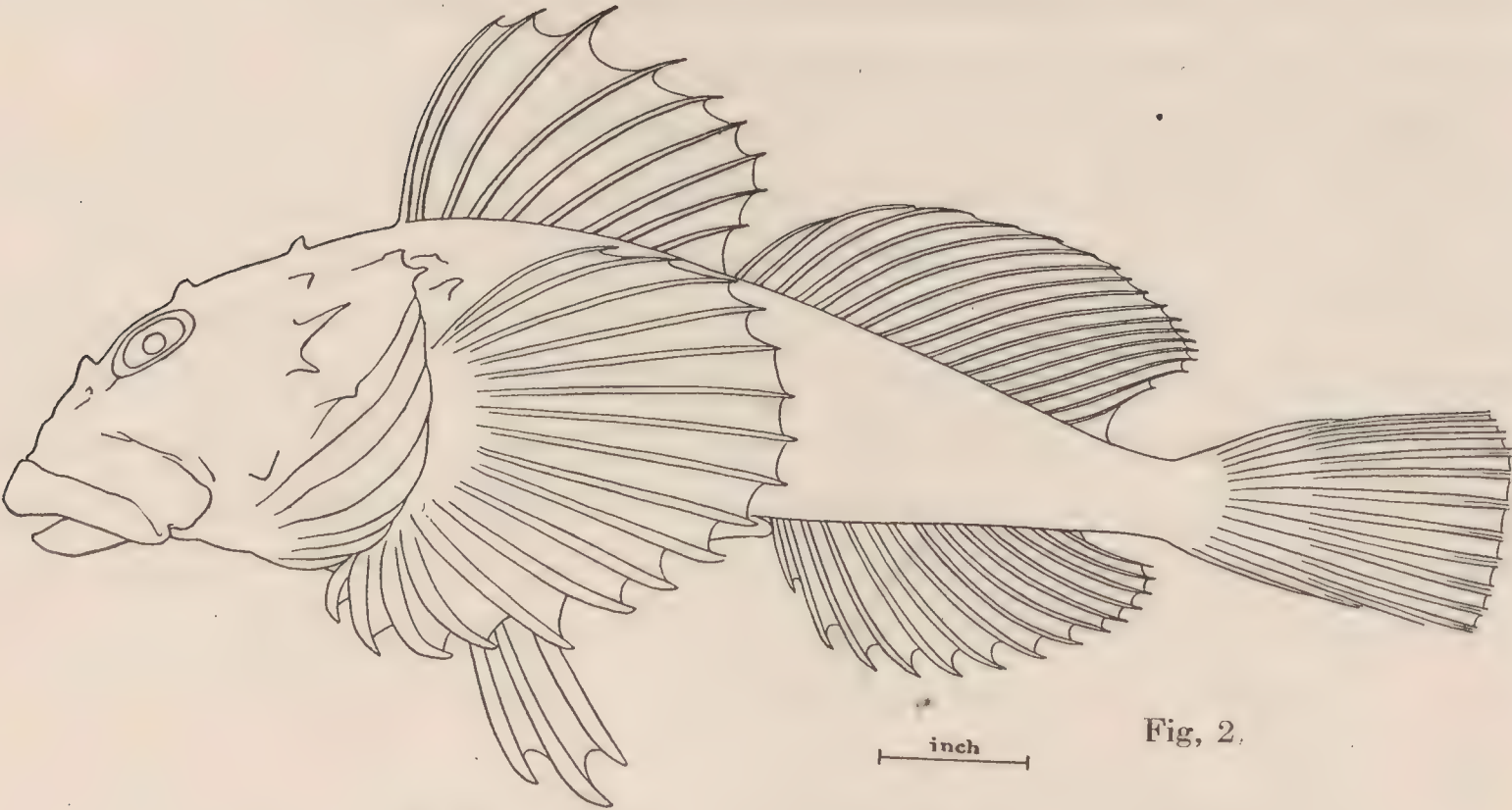


Fig. 2.

Fig. 2. *Myoxocephalus groenlandicus*, male.

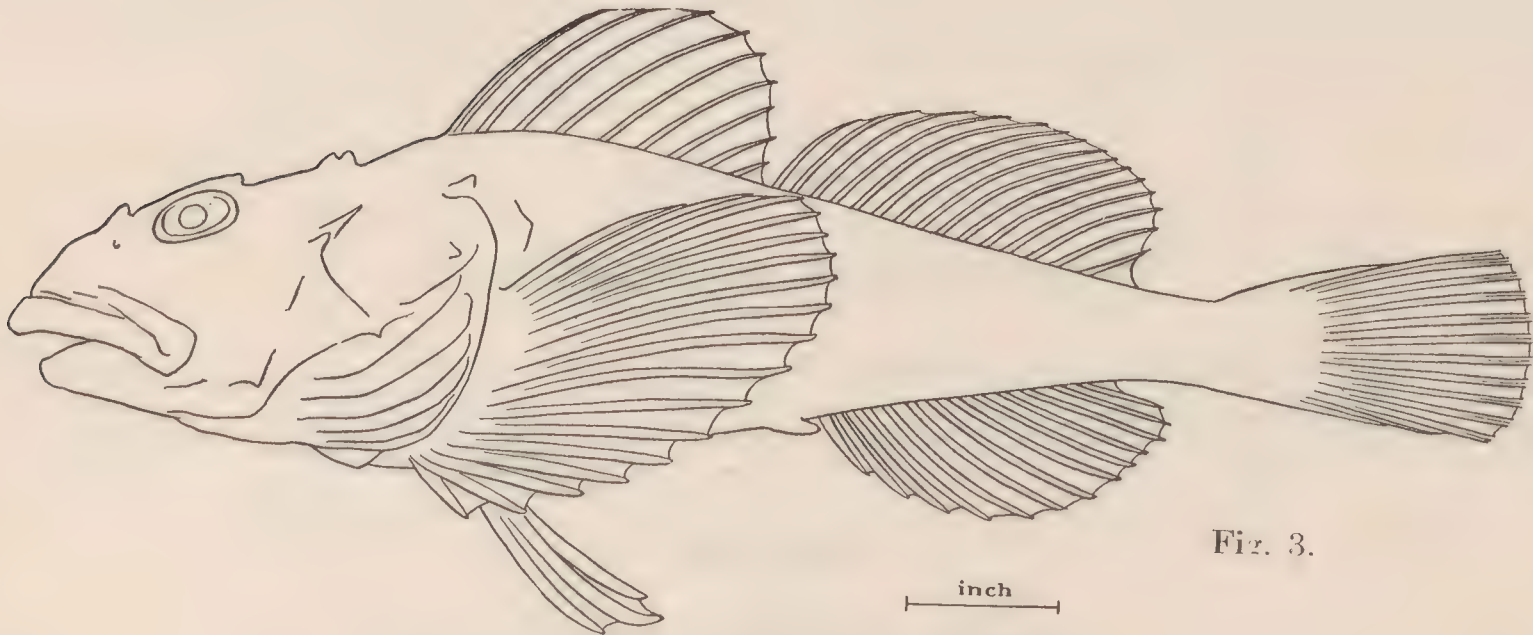


Fig. 3.

Fig. 3. *Myoxocephalus groenlandicus*, female.

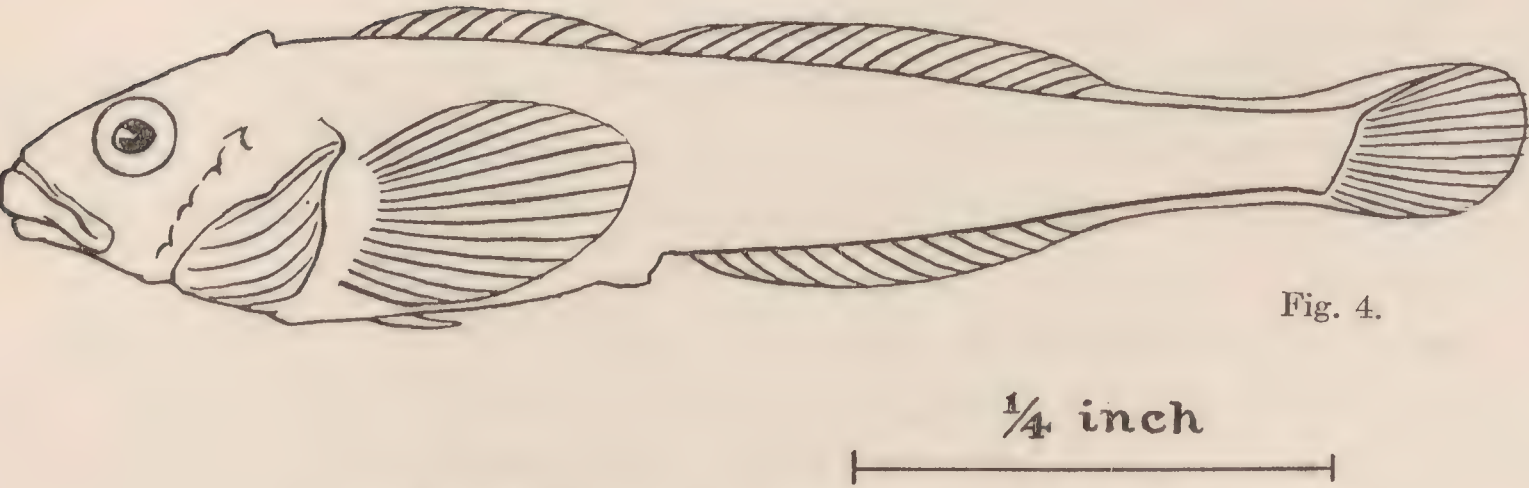


Fig. 4.

Fig. 4. *Myoxocephalus groenlandicus*, larval.

mately the same size. Both contained Crustacea, the male almost entirely small amphipods, the female more of a variety. The illustrations of these two specimens show their sexual differences.

Besides the above, there are a number of larvæ, about 19 mm. in total length, from the beach at low tide, Etah, Aug. 19, 1914, collected by Dr. Tanquery. These are in the stage figured by Johansen, (1912, Medd. om Gronl. XLV, p. 12, Pl. XLVI, figs. 11 to 13) for *Oncocottus quadricornis* and resemble these figures very closely. They have 12 clearly discernible rays in the anal fin; about X, 17 in the dorsal; no slit behind the last gill; the only evident spines at the nape, except for 4 rather well-marked ones on the preopercle (see Fig. 4). I place them provisionally with this, the most abundant adult form, although their fin rays agree most closely with *scorpioides*. It is within the realms of possibility that they are the larvæ of *Icelus bicornis*.

Fish larvæ are often specialized forms with little philogenic significance. It seems probable, however, that such free-swimming cottoid larvæ approach the ancestry of the cottoid group. It is remarkable that, though repeatedly described from the Arctic, they are unfamiliar in these latitudes (New York). Perhaps different habits here make them less accessible.

CYCLOPTERIDÆ

Eumicrotremus spinosus (Müller)

Two small specimens, between 15 and 20 mm. long to tip of caudal, from Etah, Sept. 7, 1914, taken in water between two and 10 fathoms deep.

LIPARIDÆ

Liparis tunicatus Reinhardt

There is one specimen, 45 mm. long to tip of caudal, from the beach at Etah at low tide, Aug. 19, 1914, and twenty-three of 35 to 80 mm. from *Laminaria* at Umanak in July of the same year.

The two largest of these, 75 and 80 mm., are in excellent condition for study and, on account of the scarcity of good Greenland material in collections and the several species described from this region, a description of them is here given.

Head in length to base of caudal, 3.7–3.5; depth, 4.2; eye, in head, 5.2–5.0; snout, 2.5; interorbital, 3.0; width of mouth (inside), 2.0; length sucking disk, 2.2; pectoral from center of its base, 1.4; longest dorsal ray, 2.3; longest anal ray, 2.0–2.4; caudal, 2.0; longest ray in lower pectoral lobe, 1.7–1.6.

Margin of dorsal fin even, unbroken, joining the base of the caudal at a wide angle, anal joined to caudal somewhat farther back, so that about three-fourths of the caudal above and three-fifths below is free. Pectoral not reaching anal origin. Lower pectoral lobe extending back of the disk a distance equalling the eye. Dorsal, about 41; anal, about 35.

Color in alcohol (the larger specimen) pale, becoming purplish gray on the sides anteriorly, top of the head, and chin, gray cloudings barely indicated on the posterior vertical fins and caudal. The other specimen is dark purplish gray on the back, sides and vertical fins, the latter with a little obscure pale marbling; the belly, pale.

ZOARCIDÆ

Lycodalepis mucosus (Richardson)

A single, poorly preserved specimen of this species, previously known from Northumberland Sound and Cumerland Gulf, was collected by Mr. H. J. Hunt in shallow water along-shore beyond Provision Point, Etah, July 1915. It is 310 mm. long.

Gymnelis viridis (Fabricius)

A single specimen 180 mm. in length, Umanak, July 30, 1914, from *Laminaria*. Head in length, 7. Depth in head, 1.6; eye, 5; snout and interorbital, the same; maxillary, 2.5. Anal, about 74.

GADIDÆ

Boreogadus saida (Lepechin)

There are six specimens, 120 to 220 mm. to tip of caudal, from Umanak. The larger ones are dusky in color, including fins, and slightly paler below. The smaller are brownish, obscurely mottled with paler; dorsals, caudal, and pectorals, dusky. Ventrals dusky, with a white tip; anals white, with a rather broad black margin.

Another lot of five, also from Umanak, taken in June 1914, measure 70 to 190 mm. In July 1915, the species was found to be numerous, and six (of 90 to 130 mm.), caught by Eskimos in a crack in the ice, were preserved.

***Gadus ogac* (Richardson)**

There is one small specimen, 245 mm. to tip of caudal.

This small collection from the Arctic contains three of the four dominant types of marine acanthopterygean fishes of cold northern seas. They are the free-swimming gadoids, the more or less bottom-haunting cottoids, and the eel-like species which squirm in and out of the marine vegetation or mud, here represented by zoarcids. The fourth type, not represented, is the flatfish, specialized for lying on the bottom.

It is interesting to contrast the marine ichthyfaunæ of varying latitudes (excluding deep sea fishes). The small Arctic area has plenty of fishes, by individuals, but a great paucity of species. The broad belt of cold water extending southward on our coast to Massachusetts is notable for the few dominant types: cottoids, zoarcids, etc., gadoids, and flatfish come to mind. At about the latitude of Cape Cod the ichthyfauna changes abruptly with the rise in water temperature to about 60 degrees Fahrenheit. More southern fish-types put in an appearance here than at any other point as we approach the equator. The northern factor in the ichthyfauna dwindles rapidly from here southward, and there is a steady increase in the number of species, which is much greater in the tropics than elsewhere. The following generalization is probably safe without compiling statistics. The number of types is very small in the Arctic and increases very slowly southward until the southern ichthyfauna is met with, where there is an abrupt rise, followed by gradual increase to the tropics. The number of species is also very small in the Arctic, increases in the subarctic, then more slowly until meeting the southern fauna, and then with accelerated velocity to the tropics. The number of individuals is considerable in the arctic, perhaps reaches a maximum in the northern seas, and varies locally with an indefinite tendency to decrease southward.

Whereas it is not possible to explain these faunal conditions satisfactorily, certain factors bearing on them are plain. The abundance of macroscopic plankton due to the absence of de-nitrifying bacteria in cold northern waters¹ furnishes a superabundant food supply for the large number of individual fishes. In the tropics the conditions are very permanent, unaffected by seasonal or climatic changes, and there has been a multiplication of species to take advantage of every environmental niche. Thirdly, the indirect effect of northern ice has been a very important factor in limiting, northward, environmental variety and multiplication of forms for marine

¹ Osborn, H. F., 1917. *The Origin and Evolution of Life*, p. 91.

fishes. In the Arctic the shallows, which in the south support rich ecological associations, are scoured bare by it. Glaciation has left the New England coast uniformly stripped to the bare rock, and the change in coastal character at the southern limit of glaciation has perhaps as much to do with the abrupt change from northern to southern faunæ as the corresponding increase of water temperature. The organic waste from the land brought down by rivers doubtless is an important factor in giving variety to the environment for marine ichthyfaunæ. It increases from practically nil in Arctic glaciers to a rich contribution by tropical rivers.

Northern fishes in an environment of plenty, of monotony, but of instability, have made a few broad adjustments. Tropical fishes in an environment of competition, of variety, and of stability have made an infinite number of adjustments and, while perhaps less numerous in individuals, are vastly more numerous in species.

Article XX.—BEES FROM BRITISH GUIANA

By T. D. A. COCKERELL.

In connection with the work of the Tropical Research Station of the New York Zoological Society, conducted by Mr. William Beebe, collections of insects, including bees, were made. The present report deals with a series of bees from the Bartica District, and Mr. John Tee Van, in forwarding them, states that "almost all of these bees were procured about a clump of several species of nightshades (*Solanum*), which were flowering in thinned-out jungle." I give an artificial key, which will enable one who is not a specialist in bees to separate readily each species from the rest. It will, of course, remain necessary to compare any species with a fuller account to make sure that it is not some form unrepresented in the present collection. The types of the new species and varieties from British Guiana are deposited in The American Museum of Natural History. Species marked P. are from the Penal Settlement; those marked K. occur at Kalacoon.

- The body, or some part of it, brilliant green.....1.
 No part of the body brilliant green.....11.
1. Thorax dark, with more or less purple tints, not bright green.....2.
 Thorax bright or clear green, at least in part.....4.
2. Small bee, less than 10 mm. long.....*Augochlora callichlorura*, new species.
 Large, robust bees, greatly exceeding 10 mm.....3.
3. Abdomen with the first two segments dark; tongue not extending to end of
 abdomen.....*Eufriesia pulchra* (Smith).
 Abdomen all bright green, with brassy tints; tongue extending backward far
 beyond tip of abdomen.....*Euglossa brullei* Lepeletier.
4. Hind margins of abdominal segments broadly black.
 Augochlora nigromarginata (Spinola).— P.
 Hind margins of abdominal segments green.....5.
 Hind margins of abdominal segments red or whitish; very robust bees.....10.
5. Small bee, less than 10 mm. long, the clypeus with a transverse apical ivory-
 colored band.....*Ceratina læta* Spinola.
 Larger, very robust bees.....6.
6. Tongue extending beyond abdomen posteriorly.....7.
 Tongue not extending beyond abdomen.....8.
7. Scutellum with a patch of black tomentum..*Euglossa ignita* Smith; female.
 Scutellum without a patch of black tomentum...*Euglossa ignita* Smith; male.

8. Robust bees, about 10 mm. long or a little over; scutellum with a patch of black tomentum.....*Euglossa cordata* (Linnæus).— P.
Much larger bees, a little over 20 mm. long.....9.
9. Scutellum with an obtuse median keel; posterior angles of scutellum rounded
Exærete smaragdina (Guérin).
Scutellum depressed in middle, without any keel; posterior angles of scutellum rather prominent.....*Exærete dentata* (Linné).
10. Scutellum with a patch of light fulvous tomentum; scape red.
Euglossa decorata ruficauda, new variety; female — K.
Scutellum with a patch of black tomentum; scape dark, with a pale yellow mark.....*Euglossa singularis* Mocsáry.— P.
Scutellum without a patch of tomentum; scape pale yellow in front.
Euglossa decorata ruficauda, new variety; male.
11. Very large bees, anterior wing at least 23 mm. long; integument partly or wholly ferruginous.....12.
Anterior wing less than 20 mm. long.....13.
12. Abdomen with broad black bands.
Xylocopa frontalis nitens (Lepeletier); male¹— P.
Abdomen without black bands.....*Xylocopa fimbriata* (Fabricius).
13. Wasp-like bee, with fusiform abdomen, reddish wings and red legs; three complete submarginal cells, first recurrent nervure meeting second transverso-cubital.....*Rhathymus beebei*, new species
Otherwise formed, the abdomen broad at base.....14.
14. Surface of eyes with fine short hair; first abdominal segment red, the others black; female abdomen sharply pointed.
Cælioxys ardescens Cockerell. (Hym. 6 and 138.)
Eyes not hairy; female abdomen not sharply pointed.....15.
15. Anterior wings with three complete submarginal cells.....16.
Anterior wings with submarginal cells incomplete or wanting; stingless social bees.....29.
16. Small bee, about 8 mm. long; wings beyond middle milky-white, the extreme apex dusky.....*Tetrapedia lacteipennis* Vachal.— P.
Larger bees; the wings not thus colored.....17.
17. Abdomen clear ferruginous; large robust bees.....18.
Abdomen not ferruginous; or only partly so.....19.
18. Hind legs with black hair.....*Centris personata* Smith; male.— P.
Hind legs with pale hair.....*Centris personata* Smith; female.— P.
19. Integument with at least some bluish, purplish or greenish tints; abdomen not banded; form very robust.....20.
Integument not at all metallic (very slightly in *Eulæma nigrita*, variety)....21.

¹ The female of *X. nitens* is black, with dark wings. It was not in the material sent. The female of *X. fimbriata* is also black.

20. Larger; anterior wing at least 17 mm. long; head and thorax with black hair; fourth and fifth abdominal segments purple. *Eulæma nigrita* Lepeletier.
Much smaller; cheeks densely covered with white hair; clypeus black in female, yellow in male. *Xylocopa barbata* (Fabricius).
21. Thorax and abdomen hairy; hair of thorax yellow, with a transverse black band, of abdomen black, with a transverse yellow band.
Bombus incarum Franklin.
Not thus colored. 22.
22. Clypeus with two longitudinal keels. 23.
Clypeus with a single, median longitudinal keel, sharp and extending its whole length; black bee, with black hair. *Eulæma nigrita* Lepeletier, variety; female.¹
Clypeus without any distinct keels. 25.
23. Scutellum with two large yellow marks.
Epicharis maculata barticana, new variety.— K.
Scutellum with the integument all dark. 24.
24. Second abdominal segment with a yellow mark on each side.
Epicharis affinis Smith.— P.
Abdomen with the integument all black. *Epicharis rustica* (Olivier).— P.
25. Less than 12 mm. long; wings not deep fuliginous. 26.
Over 18 mm. long; wings deep fuliginous. 27.
26. Hair bands of abdomen broad; male with long antennæ and yellow clypeus.
Florilegus barticanus, new species.
Hair bands of abdomen linear; integument of clypeus black.
Melitoma fulvifrons (Smith).
27. Hair of mesothorax and scutellum dark brown; apical part of abdomen with integument red. *Centris fusciventris* Mocsáry.— P.
Hair of mesothorax and scutellum red. 28.
28. Face with yellow markings; anterior wing about 14 mm. long.
Centris lineolata Lepeletier.
Face without yellow markings; anterior wing about 20 mm. long.
Centris atriventris Mocsáry.— P.
29. Robust bees, not less than 9 mm. long. 30.
Small, fly-like bees, not nearly 9 mm. long. 32.
30. Thorax with ferruginous hair; integument of scutellum yellow.
Melipona fasciata barticensis Cockerell, ined.— P.
Thorax with dorsal hair not ferruginous. 31.
31. Abdomen more or less reddish, at least the first segment dorsally pale red.
Melipona intermixta Cockerell, ined.— P.
Abdomen black, with narrow yellowish-white tegumentary bands; a tuft of dark red hair before each tegula. . *Melipona interrupta* (Latreille).— K.
32. Legs mainly red; clypeus yellow. *Trigona longipes* Smith.— K.
Legs and clypeus black. *Trigona* sp. (specimens imperfect).— P.

¹ A little purple can be seen at sides of abdomen, but it is easily overlooked.

NOTES AND DESCRIPTIONS

Melipona interrupta (Latreille).— In the specimen sent, the bands on second and following segments are notched above in middle, with only an obscure linear interruption.

Melipona fasciata barticensis Cockerell.— One specimen has five linear red bands on abdomen, but in another the bands are very indistinct, almost obsolete.

Melipona intermixta Cockerell.— The ground color of the first three abdominal tergites varies; in the lighter forms that of the first is pale fulvous with the shoulders blackish, of the second and third clear ferruginous.

Euglossa singularis Mocsáry.— Judging from the brief description, it appears that **E. meliponoides** Ducke is probably the same species.

Euglossa decorata Smith, var. **ruficauda**, new variety

Both sexes with abdomen ferruginous, apically more or less dusky, but the whole effect lighter and redder than typical; scutellum green with the hind margin red. Tuft on female scutellum light fulvous. The female, from Kalacoon, (Hym. 212) is the type of the variety.

Euglossa ignita Smith, var. **chlorosoma**, new variety

Green, without coppery tints, but variably suffused with purple. It is smaller than *E. piliventris*, with shorter mouth-parts, and the labrum pallid with a pair of dusky spots. A male in the U. S. Nat. Museum from Bartica, which I reported as *E. piliventris*, belongs here. Female *E. piliventris* has long yellow hairs on the anterior margin of hind basitarsus, but in *chlorosoma* the hair in this situation is black. The type of the variety is a female labelled Hym. 140. A female from Kalacoon has brassy and coppery tints on the apical part of abdomen, and must be referred to *E. ignita* proper. The type locality of *ignita* is Jamaica.

Ceratina læta Spinola. This was described from the female. The specimen sent is a male, and differs from the female in being smaller, and having a transverse band on anterior margin of clypeus, triangular marks on lower corners of face, and a large patch (emarginate above) on labrum all ivory-white. This is very like *C. viridula* Smith, which Ducke considers a synonym of *læta*, but the base of the metathorax seems to differ, and the nervures are piceous. For the present, therefore, I retain *C. viridula* as a distinct species. The female of *C. viridula*, collected by Busck in the Panama Canal Zone, is also distinguishable from that sex of *C. læta*.

Epicharis maculata var. **barticana**, new variety

♀.—Base of mandibles with a large cuneiform yellow mark; a broad black band down each side of labrum; yellow spots on prothorax large; scutellum with a pair of large transversely oval yellow areas, separated by a narrow black band; band on second abdominal segment with a posterior median projection. Kalacoon, 1916. (Hym. 217.)

Rhathymus beebei, new species

♀.—Length about 22 mm., anterior wing 18 mm.; head clear ferruginous, with red hair, lower part of face more pallid, with a creamy tint; apical half of mandibles black; clypeus prominent, minutely roughened, with a smooth median line; mesothorax black, with a median ridge, the surface on each side of this strongly punctured, but shining between the punctures; rest of thorax ferruginous, and all of thorax with ferruginous hair; scutellum not bigibbous, but with an elevated transverse ridge; pleura with a blackish area below the wings; lower part of mesopleura with a shining tubercle; tegulae clear ferruginous, finely punctured; wings strongly reddened; legs clear ferruginous; abdomen fusiform, shining; first two segments dull reddish, pallid posterolaterally, the others reddish black, with the hind margins redder; apical plate very large, concave. Bartica District (Hym. 19). Very distinct by the transverse straight ridge on scutellum; nearest perhaps to the considerably smaller *R. unicolor* Smith, but that has dark fuscous wings. The antennae are unfortunately missing.

Augochlora callichlorura, new species

♀.—Length a little over 7 mm.; first two abdominal segments rather weakly vibrissate on hind margin with orange hairs; hind spur of hind leg with long spines. Head and thorax very dark purplish, nearly black, but a blue-green spot at upper end of clypeus, supraclypeal area brilliant purple, and base of metathorax strongly tinged with purple; anterior and middle legs dark, with weak purple tints, but hind femora, tibiae and basal half of basitarsi all brilliant green on outer side; abdomen short and broad, shining, very brilliant emerald green. Head broad, eyes strongly converging below; clypeus with extremely large punctures; front dull and granular; ocelli ordinary; cheeks with thin white hair; mesothorax and scutellum shining, but well punctured; base of metathorax with strong short plicae; angles of prothorax not prominent; tegulae rufotestaceous; wings grayish translucent, stigma and nervures dusky pale brown; first recurrent nervure meeting second transversocubital; abdomen with thin pale hair, hind margins of segments not darkened. Bartica District.

Unique by the combination of purplish head and thorax and green abdomen, the general effect recalling *A. atropos* Smith.

Florilegus barticanus, new species.

♂.—Length about 11 mm.; black, except as follows: first abdominal segment strongly greenish; clypeus and labrum entirely yellow; mandibles fulvous apically (but base black); antennæ, except the first two joints, ferruginous beneath; hind tarsi, and apex of hind tibiæ, dusky red; hair of head and thorax ferruginous, paler below, no admixture of dark hairs; eyes reddish; mesothorax shining, but distinctly punctured; tegulæ clear ferruginous; wings dusky hyaline, nervures reddish fuscous; legs with pale hair, conspicuously plumose on hind tibiæ; abdomen with four broad dense ochraceous hair-bands, that on fourth segment broadly excavated in middle posteriorly, on fifth broadly interrupted; sixth segment with a small patch of fulvous hair on each side; apical part of abdomen dorsally, except for the bands and patches, with very dark fuscous hair. Bartica District (Hym. 11).

Related to *F. lanieri* Guér. from Cuba and *F. condigna* Cresson from the United States. In the coloration of the legs it is intermediate between these two.

Tetrapedia lacteipennis Vachal.—It should be added to Vachal's description, that the dorsal abdominal segments 2 to 4 have yellow bands.

The Bartica collection contains a *Megalopta* from Hoorie, but it is unfortunately broken. I have *Megalopta panamensis* Cockerell from Maroni, French Guiana (Queensland Museum, 42).

I add the description of a new species from French Guiana, the type of which is in my collection.

Augochlora maroniana, new species

♀.—Length slightly over 8 mm.; head, thorax and legs bright green; abdomen yellowish green strongly suffused with coppery, the first two segments with apical fringes of orange hair; face rather narrow; antennæ black; lower middle of clypeus black; mesothorax and scutellum rough with dense punctures, the scutellum with two copper-red spots; area of metathorax with very feeble plicæ; tegulæ black with pallid margin, the basal side broadly green; wings dusky; second s. m. square; first r. n. meeting second t. c.; stigma dusky reddish; legs with mainly pale hair, hind tibiæ with dark hair on outer side basally; hind spur with about six long spines; basal half of basitarsi green on outer side; abdomen shining, with pale ochreous hair.

Maroni, French Guiana (Queensland Mus., 43). Related to *A. cupreola* (Ckll.), but with the vibrissate fringes on abdomen nearly twice as long, and deep orange-fulvous, and the mesothorax much more densely punctured. Also related to *A. diversipennis* (Lep.), but with the face much narrower, and the area of metathorax much less distinctly plicate. From *A. calypso* Sm. it is known by the wings not being yellowish, the inner orbits not edged with blue, and the tarsi not ferruginous.

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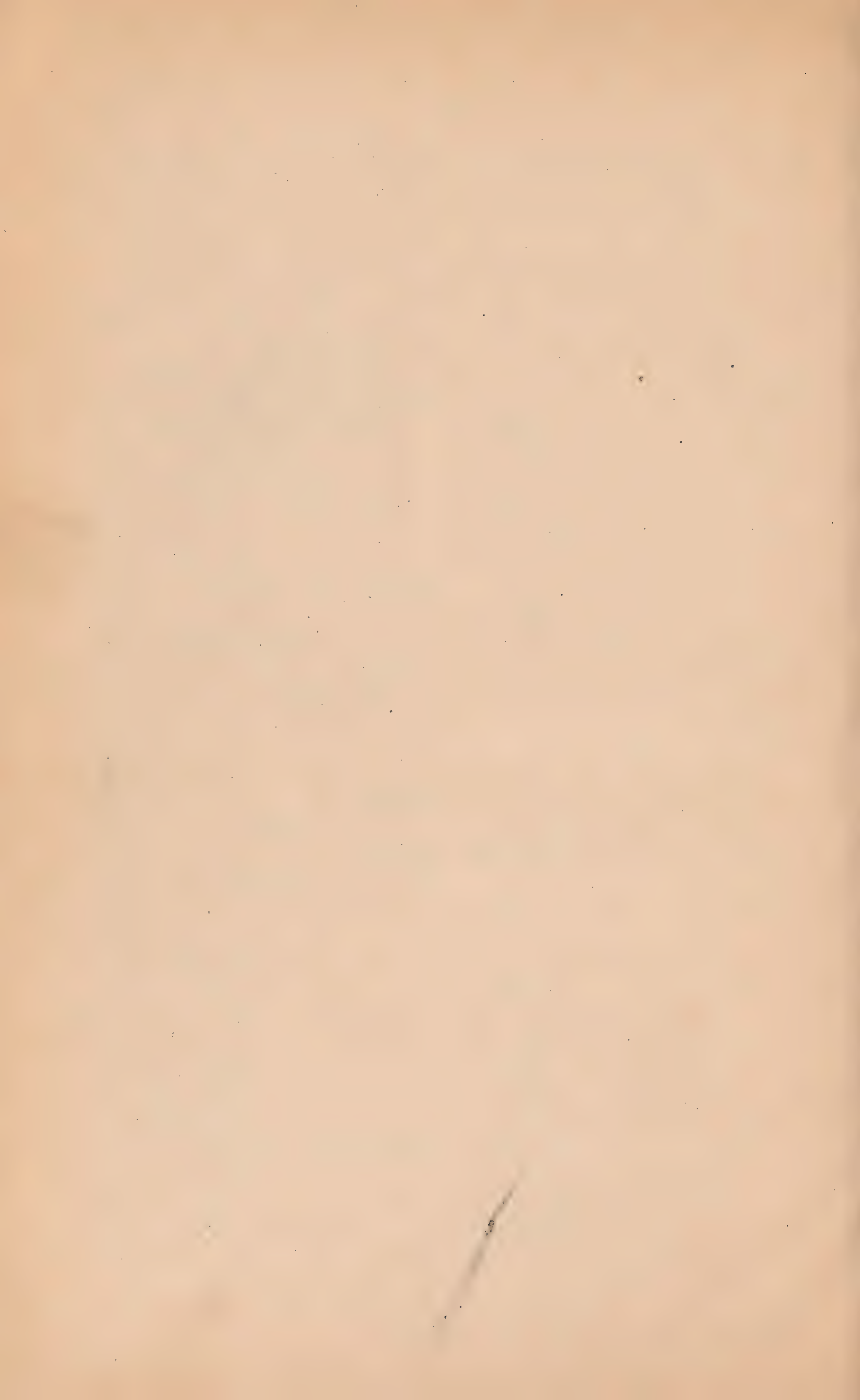
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